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**Brigham Young University
Science Bulletin**

**TICKS OF THE NATIONAL
REACTOR TESTING STATION**

by
DORALD M. ALLRED



BIOLOGICAL SERIES — VOLUME X, NUMBER 1

JUNE 1968

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TICKS OF THE NATIONAL REACTOR TESTING STATION¹

by

Dorald M. Allred

INTRODUCTION

Ecological investigations by Brigham Young University were begun at the National Reactor Testing Station in June, 1966, and were continuous until September, 1967. Although emphasis was on the study of ectoparasites, other related studies conducted as time permitted yielded additional data on the ecology of the vertebrate hosts and some of the free-living arthropods. These studies are part of an inventory and ecological survey of the native animals which occur on and adjacent to nuclear testing stations. These investigations, those begun at the Nevada Test Site by BYU in 1959 (Allred, Beck, and Jorgensen, 1963), and those being carried on by other institutions will provide a basis for evaluation of the effects of nuclear testing on native animals relative to the economy and welfare of man.

I am indebted to my former associate, D Elden Beck, who contributed a great deal before his untimely death in August, 1967. The field studies were efficiently performed by Clyde L. Pritchett, formerly of Ricks College and now a faculty member of the Department of Zoology and Entomology, BYU; Robert L. Amoureux, formerly a biology teacher in the Payette and Pocatello public schools; Gerald Richards, formerly a graduate student at BYU, now at Wisconsin State University, Whitewater; Eugene McKennie, formerly a graduate student

at BYU, now with the Westinghouse Corporation, Idaho Falls; and Duane Atwood, graduate student in the Botany Department, BYU. C. Lynn Hayward, Department of Zoology and Entomology, BYU, assisted in field studies of the birds, and identified reference collections of the birds and mammals. Wilmer W. Tanner, Department of Zoology and Entomology, BYU, verified the identifications of the amphibians and reptiles. Joseph R. Murdock, Department of Botany, BYU, identified the plant types in our major study areas.

The ticks were identified by Jose Merino, University of Wisconsin, Milwaukee, and Richard Ashley, Department of Zoology and Entomology, BYU. Some identifications and verifications were made by Carleton Clifford, Rocky Mountain Laboratory, Hamilton, Montana.

Financial support for the project was provided by the U. S. Atomic Energy Commission, Contract AT(11-1)-1559. Logistics were arranged by personnel of the AEC operations office in Idaho Falls and at the National Reactor Testing Station, specifically Courtney D. Scott, Preston Brimhall, and Ralph Batie.

I am indebted to many laboratory technicians, particularly Jane Ashley, Sylvia Child, and Connie Donaldson, for preparation of the ectoparasites for identification.

PHYSICAL CHARACTERISTICS

The National Reactor Testing Station (NRTS) is situated in southeastern Idaho, with its southeastern boundary approximately 30 miles west of Idaho Falls (Fig. 1). Most of the station lies in Butte County, with extensions into Bingham, Bonneville, Jefferson, and Clark Counties (Fig. 2). It covers an area of approximately

894 square miles, and extends for about 39 miles north and south and 36 miles from east to west in its longest dimensions (U. S. AEC, 1965).

The station is situated on a level plain with an average elevation of 4865 ft. This is part of the Snake River Plain section of the Columbia Plateaus province. The station is bordered on

¹BYU-AEC Report No. C00-1559-1.

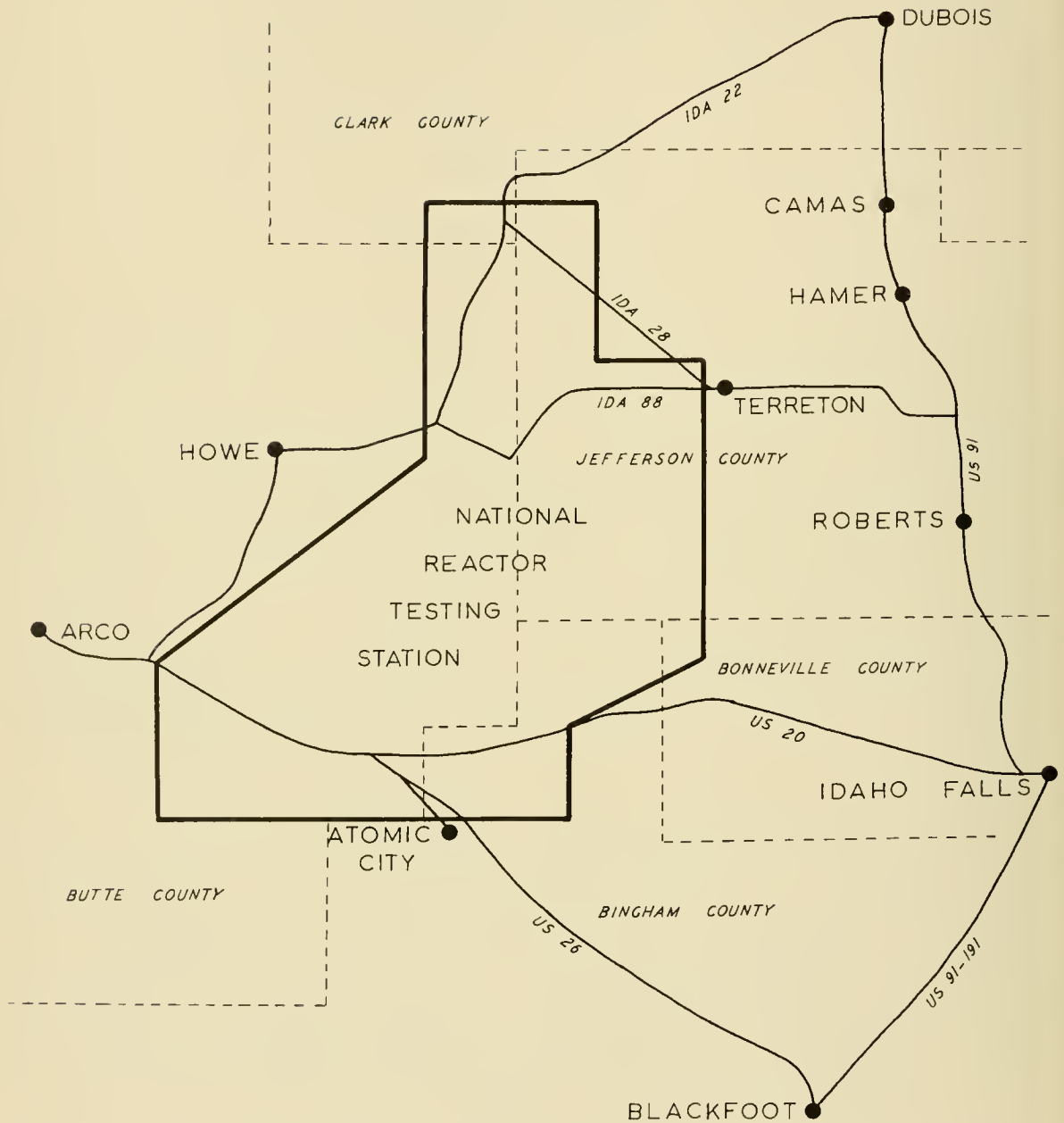


Fig. 1. Location of the National Reactor Testing Station in relationship to some cities in southeastern Idaho.

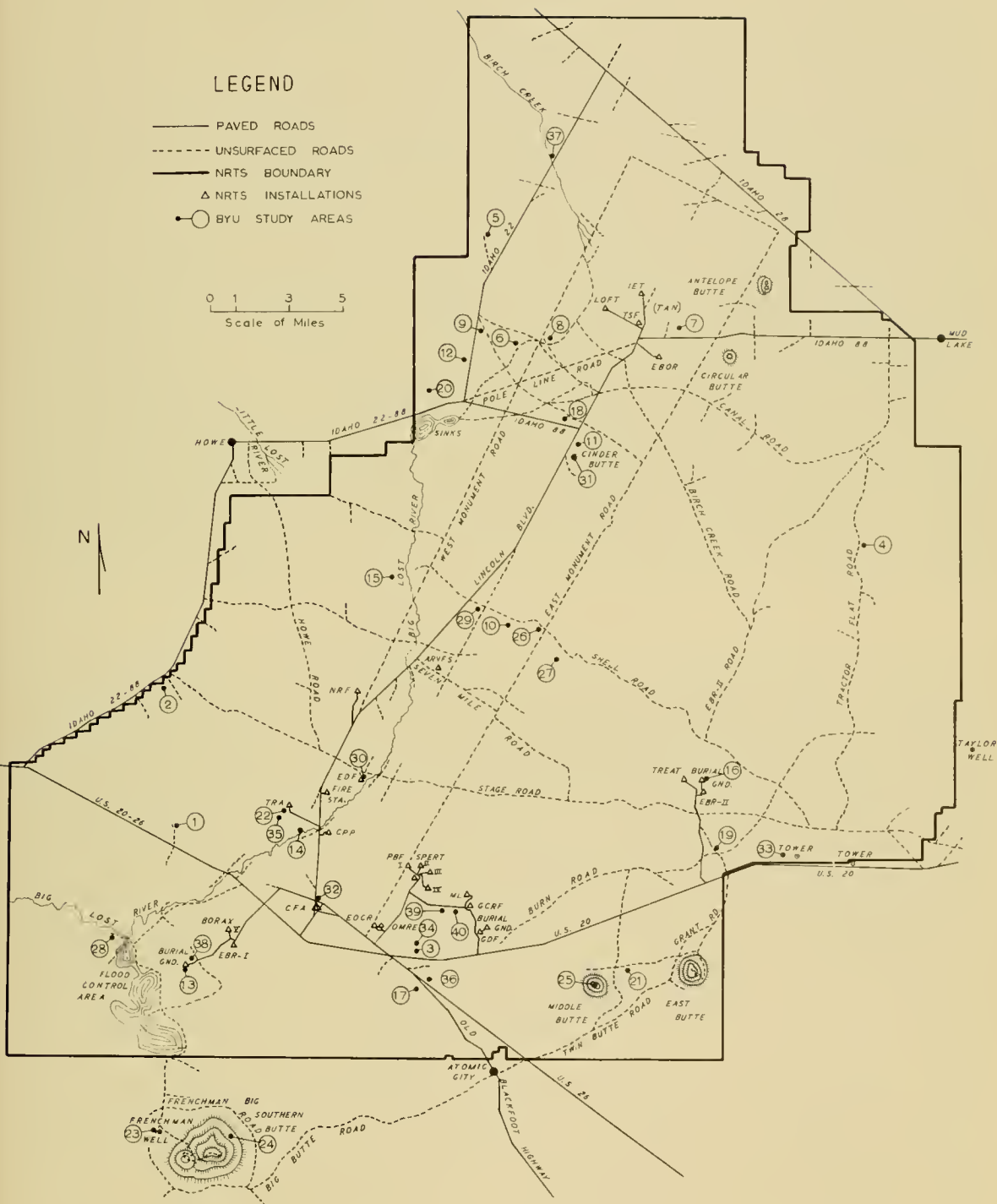


Fig. 2. Principal study areas at the National Reactor Testing Station.



Fig. 3. Lemhi Mountains at the northwestern edge of the National Reactor Testing Station.



Fig. 4. Big Lost River during time of spring run-off.



Fig. 5. Sinks area in the northwestern part of the station.



Fig. 6. Mouth of volcanic cave, study area 19.



Fig. 7. Mouth of volcanic cave, study area 21.

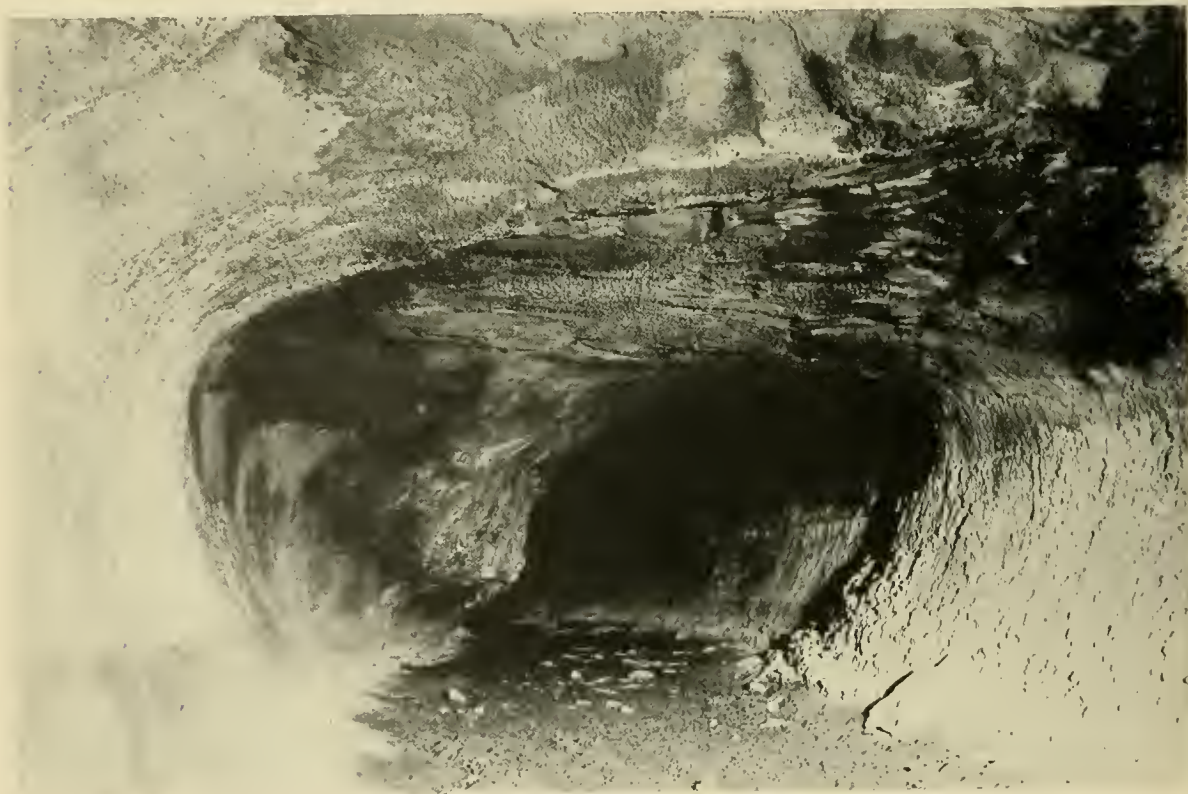


Fig. 8. Inside of volcanic cave, study area 21. Height of ceiling at this point is approximately 12 ft.

the north and west by the Bitterroot, Lemhi, and Lost River Mountains (Fig. 3). On the east and south the topography is typical of the plainlike area of the Snake River drainage and the Great Basin. Little Lost River, Birch and Camas Creeks barely reach and drain into the northern areas of the station. Big Lost River enters from the southwest, traverses more than half the north-south distance, and drains into the sinks of the north-central portion (Figs. 4 and 5).

The central and southern parts of the station are typified by basalt flows which are exposed or covered by only a few feet of soil. The northern section is primarily lake and eolian deposits, and basalt flows are less common. The basalt flows are from earliest Pleistocene to Recent, some dating perhaps as recent as 2000 years (Bates, 1965). Rising above the basalt flows at the southern part of the station are three prominent buttes towering 1000 ft or more above the landscape—East, Middle, and Big Southern Buttes. Typical of many volcanic areas, the

basalt flows are honeycombed with caves of various sizes and degrees of accessibility (Figs. 6 to 9).

Annual precipitation at the station averages less than 10 inches. The average annual temperature is 42 degrees, with extremes of 102 and minus 43 degrees F (U. S. AEC, 1965). Prevailing breezes are typical of the area.

The vegetation of the NRTS is characteristic of the cool, northern desert shrub type biome. The most conspicuous plant over most of the area is sagebrush, *Artemisia tridentata*. Other predominant plants are rabbitbrush, *Chrysothamnus* sp., and grasses of several genera—*Agropyron*, *Elymus*, *Oryzopsis*, and *Stipa*. McBride prepared a vegetation map of the NRTS on which he designated 19 major plant communities (Fig. 10). Detailed plant analyses of our permanently established study areas vary somewhat from McBride's designations; however, reference is made to his types for correlation with his map.

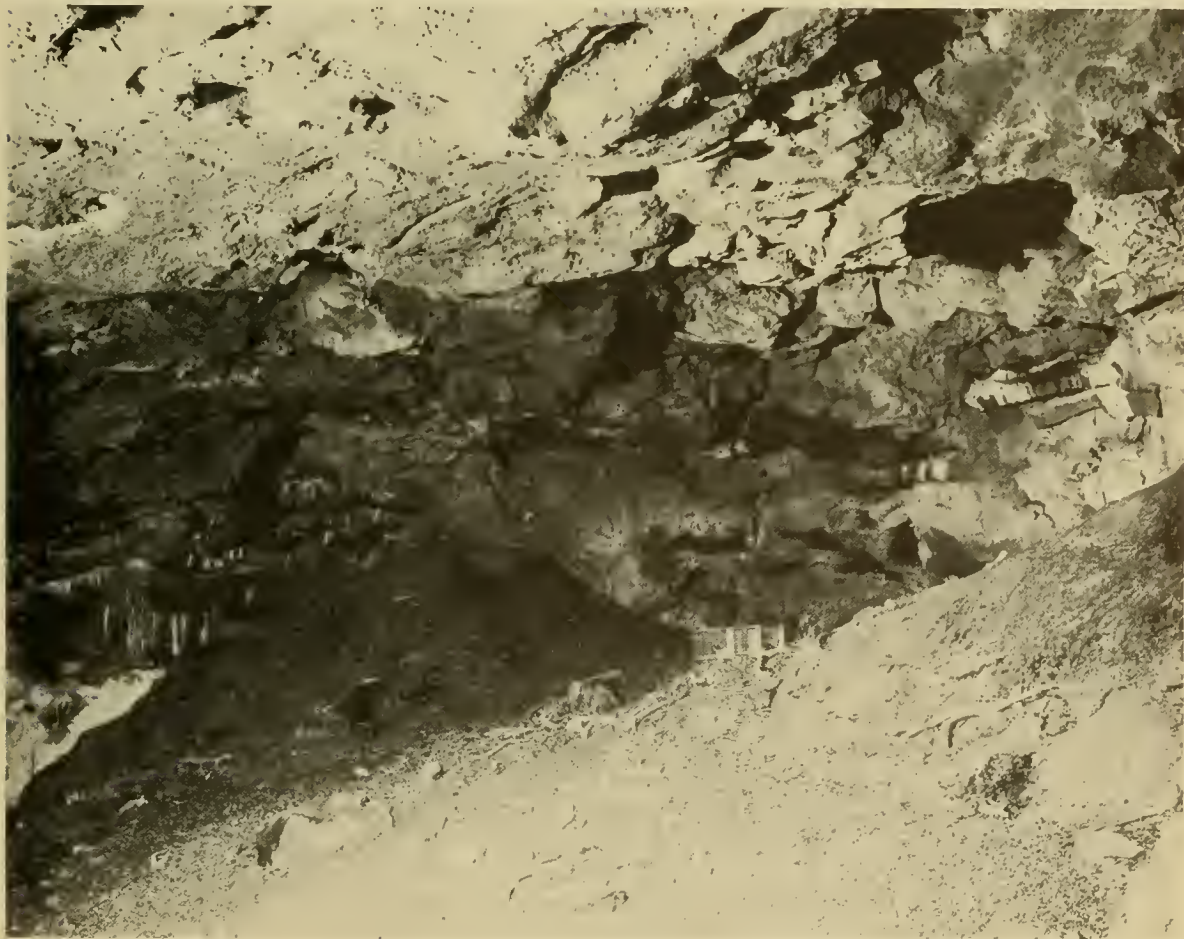


Fig. 9. Inside of volcanic cave, study area 33. Height of ceiling at this point is approximately 7 ft. Mounds at front and back center, and right foreground are piles of woodrat excreta, each several feet deep.

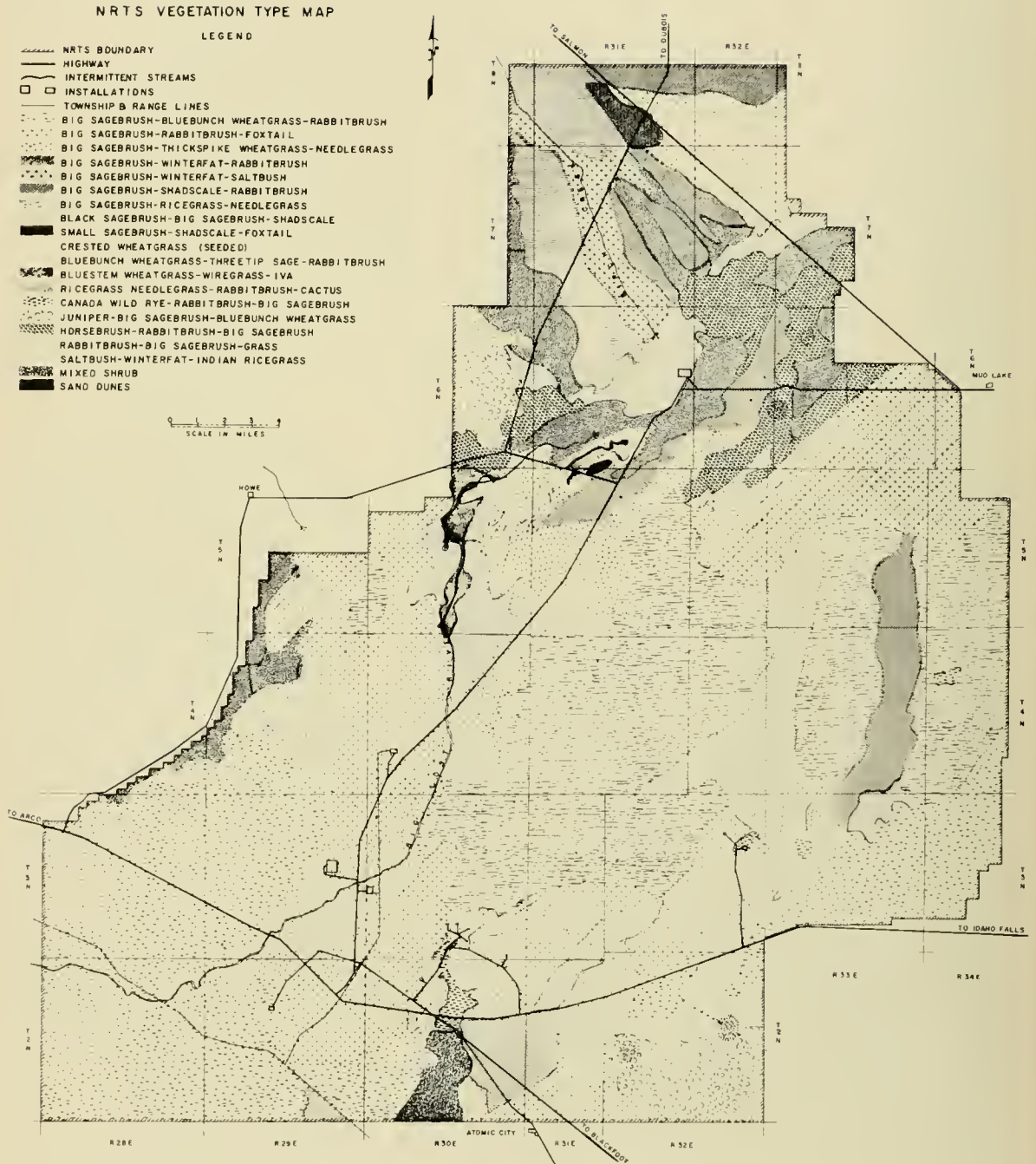


Fig. 10. Major plant types as designated by McBride. Reproduced by permission of Ray McBride, Atomic Energy Comm., Idaho Falls.

STUDY AREAS

Twelve primary sites (Areas 1 to 12) were studied periodically in the major vegetation types of the NRTS, and 28 secondary areas were studied at less regular intervals (Fig. 2). These latter areas were chosen because of their atypical nature in relationship to the extensive vegetative types.

Area 1. Two miles west of Big Lost River bridge along highway US 20-26, thence 0.7 mile north-northwest along old paved highway, thence 100 yards north of road (Fig. 11). This is designated as a *Chrysothamnus*-*Artemisia* community, and occurs in McBride's Big Sagebrush-Bluebunch Wheatgrass-Rabbitbrush type. Plant analysis: *Chrysothamnus* 38%; *Artemisia* 24%; grasses (*Oryzopsis*, *Sitanion*, *Stipa*) 15%;

forbs (*Allium*, *Astragalus*, *Descurainia*, *Eriogonum*, *Lappula*, *Lupinus*, *Umbelliferae*, *Zigadenus*) 10.5%; *Opuntia* 6%; *Tetradymia* 1.5%; bare ground 5%.

Area 2. Six miles northeast of junction of highways Idaho 22-88 and US 20-26 along highway Idaho 22-88, thence 125 yards east of road (Fig. 12). This *Artemisia*-*Chrysothamnus* community occurs in McBride's Big Sagebrush-Winterfat-Rabbitbrush type. Plant analysis: *Artemisia* 50%; *Chrysothamnus* 15%; grasses (*Agropyron*, *Oryzopsis*, *Poa*, *Stipa*) 15%; *Eurotia* 10%; forbs (*Astragalus*, *Castilleja*, *Cryptantha*, *Erigeron*, *Eriogonum*, *Lupinus*) 7%; bare ground 3%.



Fig. 11. Study area 1. Predominant plants are *Chrysothamnus* and *Artemisia*.



Fig. 12. Study area 2, with twin buttes in the background. Predominant plant is *Artemisia*.

Area 3. One mile east of junction of highways US 20-26 along highway US 20, thence 100 yards north of road (Fig. 13). This *Elymus* community is in McBride's Canada Wild Rye-Rabbitbrush-Big Sagebrush type. Plant analysis: *Elymus* 50%; forbs and grass (*Allium*, *Mentzelia*, mustards, *Phlox*, *Sitanion*, *Vicia*) 35%; bare ground 15%.

Area 4. Along highway Idaho 88, 2.25 miles west of Mud Lake (City), thence south of highway 8 miles along Tractor Flat Road (Fig. 14). This site is designated as an *Oryzopsis-Stipa* community, and occurs in McBride's Ricegrass-Needlegrass-Rabbitbrush-Cactus type. Plant analysis: *Oryzopsis* 50%; *Stipa* 40%; shrubs 5%; forbs 5%.

Area 5. Along highway Idaho 22, 5.2 miles north of its junction with highway Idaho 88, thence 0.6 mile northwest from road (Fig. 15). This is a *Juniper* (without understory) community which occurs in McBride's *Juniper*-Big Sagebrush-Bluebunch Wheatgrass type. Plant analysis: *Juniperus* 40%; forbs 1%; bare ground 59%.

Area 6. One mile northeast of junction of highways Idaho 22 and 88 along Pole Line Road, thence north 2 miles along old road (Fig. 16). *Chrysothamnus-Tetradymia* community occurs in McBride's Horsebrush-Rabbitbrush-Big Sagebrush type. Plant analysis: *Chrysothamnus* 30%; *Tetradymia* 30%; *Artemisia* 20%; grasses (*Agropyron*, *Oryzopsis*, *Stipa*) 5%; forbs (As-



Fig. 13. Study area 3, with twin buttes in the background. Predominant plant is *Elymus*.



Fig. 14. Study area 4. Predominant plants are *Oryzopsis* and *Stipa*.



Fig. 15. Study area 5. Predominant plant is *Juniperus*.



Fig. 16. Study area 6, with Lemhi Mtns. in the background. Predominant plants are *Chrysothamnus*, *Tetradymia*, and *Artemisia*.

tragalus, *Eriogonum*, *Medicago*) 5%; bare ground 10%.

Area 7. One and one-half miles east of NRTS facility TAN along highway Idaho 88, thence 0.3 mile north of highway (Fig. 17). This *Chrysothamnus*-*Artemisia* community occurs in McBride's Big Sagebrush-Winterfat-Rabbitbrush type. Plant analysis: *Chrysothamnus* 41%; *Artemisia* 30%; *Eurotia* 9%; forbs and grasses (misc. grasses and *Salsola kali*) 4%; bare ground 16%.

Area 8. One mile northeast of junction of highways Idaho 22 and 88 along Pole Line Road, thence north 3 miles along old road (Fig. 18). *Artemisia*-*Atriplex* community occurs in McBride's Big Sagebrush-Winterfat-Rabbitbrush type. Plant analysis: *Artemisia* 30%; *Atriplex* 26%; *Chrysothamnus* 5%; forbs and grasses (misc. grasses, *Penstemon*, *Phlox*) 1%; bare ground 38%.

Area 9. Two and eight-tenths miles north of junction of highways Idaho 22 and 88 along highway 22, thence 0.2 mile east of highway (Fig. 19). This *Chenopodium*-*Eurotia* community occurs in McBride's Rabbitbrush-Big Sagebrush-Grass type. Plant analysis: *Chenopodium* 40%; *Eurotia* 35%; *Artemisia* and *Chrysothamnus* 2%; *Salsola* 2%; forbs 1%; bare ground 20%.

Area 10. Five miles northeast of NRTS facility NRF along Lincoln Blvd., thence east 1.8 miles along Shell Road, thence 125 yards south of road (Fig. 20). This *Artemisia* community occurs in McBride's Big Sagebrush-Ricegrass-Needlegrass type. Plant analysis: *Artemisia* 68%; *Opuntia* 7%; grasses (*Agropyron*, *Oryzopsis*, *Stipa*) 7%; forbs (*Astragalus* *Sphaeralcea*, *Umbelliferae*) 5%; bare ground 13%.

Area 11. Along Lincoln Blvd., 0.5 mile south of its junction with highway Idaho 88, thence 220 yards east of Lincoln Blvd. (Fig. 21). *Chrysothamnus*-Grass-Tetradymia community occurs in McBride's Ricegrass-Needlegrass-Rabbitbrush-Cactus type. Plant analysis: *Chrysothamnus* 30%; grasses (*Agropyron*, *Oryzopsis*, *Stipa*) 26%; *Tetradymia* 22%; *Artemisia* 5%; *Opuntia* 5%; forbs (*Allium*, *Astragalus*, *Comandra*, *Eriogonum*, *Gilia*, *Lupinus*, *Phlox*) 5%; *Atriplex* 2%; bare ground 5%.

Area 12. Along highway Idaho 22, 1.5 miles north of its junction with highway Idaho 88, thence 175 yards west of highway (Fig. 22). Juniper (with understory) community occurs in McBride's Juniper-Big Sagebrush-Bluebunch Wheatgrass type. Plant analysis: *Juniperus* 30%; *Chrysothamnus* 15%; *Eurotia* 15%; *Artemisia*

13%; grasses (*Oryzopsis*, *Stipa*) 10%; forbs (*Chenopodium*, *Eriogonum*, *Mentzelia*, *Salsola*) 6%; *Opuntia* 1%; bare ground 10%.

Area 13. Nuclear waste burial ground 2 miles southwest of NRTS facility EBR-I. This is in McBride's Big Sagebrush-Bluebunch Wheatgrass-Rabbitbrush type.

Area 14. One-half mile west of Lincoln Blvd. along Big Lost River south of NRTS facility TRA. This is in McBride's Big Sagebrush-Thickspike Wheatgrass-Needlegrass type.

Area 15. Grassy sinks area west of Big Lost River, near its junction with Shell Road, 3.5 miles west of Lincoln Blvd. This is in McBride's Bluestem Wheatgrass-Wiregrass-Iva type.

Area 16. Nuclear waste burial ground 0.5 mile north of NRTS facility EBR-II. This is in McBride's Big Sagebrush-Rabbitbrush-Foxtail type.

Area 17. Along highway US 26 one mile southeast of its junction with highway US 20, thence 0.6 mile south-southeast along old Blackfoot Highway, thence west to lava flow. Situated in McBride's Mixed Shrub type.

Area 18. The sand dunes area is situated immediately north of highway Idaho 88 approximately 0.6 mile west of its junction with Lincoln Blvd. (Fig. 23).

Area 19. This cave is situated south of NRTS facility EBR-II (Fig. 6). Proceed north from highway US 20 for 0.2 mile from its junction with Grant Road. At this point take the left fork and proceed for an additional 0.8 mile to the cave which is on the east side of the road. This is in McBride's Big Sagebrush-Rabbitbrush-Foxtail type.

Area 20. The west-facing side of a rocky outcrop may be reached by proceeding westward along a dirt road that extends to the top of the hill west of the junction of highways Idaho 22 and 88. This is in McBride's Juniper-Big Sagebrush-Bluebunch Wheatgrass type.

Area 21. This cave is situated slightly to the north of and between East and Middle Buttes (Fig. 7). Proceed south from highway US 20 along a dirt road, which junctures near highway US 20 mileage post 295, until an eastward road extending along the northern sides of the buttes is reached. Turn east and proceed for approximately 0.4 mile to a road which extends southward for a short distance to the cave.

Area 22. A reservoir is situated adjacent to NRTS facility TRA. This is in McBride's Big



Fig. 17. Study area 7. Predominant plants are *Chrysothamnus* and *Artemisia*.



Fig. 18. Study area 8, with Lemhi Mtns. in the background. Predominant plants are *Artemisia* and *Atriplex*.



Fig. 19. Study area 9, with twin buttes in the background. Predominant plants are *Chenopodium* and *Eurotia*.



Fig. 20. Study area 10. Predominant plant is *Artemisia*.



Fig. 21. Study area 11. Predominant plants are *Chrysothamnus*, grasses, and *Tetradychia*.



Fig. 22. Study area 12. Predominant plants are *Juniperus*, *Chrysothamnus*, *Eurotia*, and *Artemisia*.



Fig. 23. Sand dunes (study area 18) with predominant fringing plant, *Salsola*.

Sagebrush - Thickspike Wheatgrass - Needlegrass type.

Area 23. Frenchman's Well is situated adjacent to a cabin, west-northwest of and approximately 0.5 mile from Big Southern Butte. This may be reached by proceeding from the area of NRTS facility EBR-I to the peripheral road which encircles Big Southern Butte and its junction with the road which proceeds to the top of the butte.

Area 24. Webb Springs is situated on the east-northeast slope of Big Southern Butte. The canyon where the spring occurs has a dense growth of aspen and other trees. It may be reached by proceeding along the peripheral road which encircles the butte.

Area 25. Top and slopes of Middle Butte. This butte is entirely basalt with mixed brush and junipers. It occurs in McBride's Juniper-Big Sagebrush-Bluebunch Wheatgrass type.

Area 26. A lava outcrop is situated 3.5 miles along Shell Road east of its junction with Lincoln Blvd. This is in McBride's Big Sagebrush-Ricegrass-Needlegrass type.

Area 27. A volcanic sink may be reached by proceeding eastward along Shell Road for 4.1 miles from its junction with Lincoln Blvd., thence along the right fork for an additional 0.5 mile. This is in McBride's Big Sagebrush-Ricegrass-Needlegrass type.

Area 28. A burned area situated in McBride's Big Sagebrush-Bluebunch Wheatgrass-Rabbitbrush type. Proceed south along a dirt road, which junctures with highway US 20-26

east of mileage post 279, until the road crosses a railroad track. Turn right and proceed along the dike until the road crosses a dam on the Big Lost River. Approximately 300 yards further west the burned area is situated on the south side of the river.

Area 29. A lava outcrop is situated along Shell Road, 0.4 mile east of its junction with Lincoln Blvd. This is in McBride's Big Sagebrush-Thickspike Wheatgrass-Needlegrass type.

Area 30. The Experimental Dairy Farm may be reached by proceeding north from NRTS facility CFA along Lincoln Blvd. for 5.8 miles, thence east along Stage Road for 1.7 miles. This is in McBride's Big Sagebrush-Thickspike Wheatgrass-Needlegrass type.

Area 31. Cinder Butte is situated a short distance east of Lincoln Blvd., about 0.5 mile south of its junction with highway Idaho 88. This is on the line between McBride's Ricegrass-Needlegrass-Rabbitbrush-Cactus and Big Sagebrush-Thickspike Wheatgrass-Needlegrass types.

Area 32. At the north edge of NRTS facility CFA is an area occupied by huge concrete blocks formerly used as targets for naval ordnance. The plants are predominantly *Artemisia*, *Chrysothamnus*, and *Salsola*, with few annuals. This occurs on the border between McBride's Big Sagebrush-Rabbitbrush-Foxtail and Big Sagebrush-Thickspike Wheatgrass-Needlegrass types.

Area 33. This volcanic cave is situated approximately 200 yards north of highway US 20, three miles east from its junction with the road

that proceeds north to NRTS facility EBR-II (Fig. 9). This is in McBride's Big Sagebrush-Bluebunch Wheatgrass-Rabbitbrush type.

Area 34. This area is approximately 300 yards north of study area 3. It is on the borderline of the Canada Wild Rye-Rabbitbrush-Big Sagebrush and Big Sagebrush-Rabbitbrush-Fox-tail types of McBride.

Area 35. The *Salix* community is situated 200 yards southwest of the reservoir near NRTS facility TRA. It occurs in McBride's Big Sagebrush-Thickspike Wheatgrass-Needlegrass type.

Area 36. This area extends over a linear distance of approximately six miles, but is centered alongside the old Blackfoot Highway, about 4 miles north of Atomic City. The predominant vegetation is *Elymus*, *Artemisia*, and *Chrysothamnus*. It is situated in McBride's Crested Wheatgrass type.

Area 37. Proceed nine and one-half miles northeast of the junction of highways Idaho 22-88 along highway Idaho 22 to a point approximately 200 yards north of Birch Creek, thence

west 250 yards from paved road. Predominant plants are *Artemisia*, *Chrysothamnus*, and *Prunus* (Chokecherry) along the creek. This is in McBride's Black Sagebrush-Big Sagebrush-Shadscale type.

Area 38. This area is 0.3 mile northeast of the burial grounds which lie southwest of NRTS facility EBR-I. The predominant plants are *Agropyron* with some *Artemisia*. This is in McBride's Big Sagebrush-Bluebunch Wheatgrass-Rabbitbrush type.

Area 39. This area is 0.8 mile west of NRTS facility GCRF along paved road (Wilson Blvd.), thence 0.1 mile south of highway in a lava outcrop. The predominant vegetation is *Artemisia*. This area is in McBride's Big Sagebrush-Rabbitbrush-Foxtail type.

Area 40. This area is 0.3 mile west of NRTS facility GCRF along paved road (Wilson Blvd.), thence 0.1 mile south of highway in a lava outcrop. The predominant vegetation is *Artemisia*. This area is in McBride's Big Sagebrush-Rabbitbrush-Foxtail type.

PROCEDURES

Vertebrate Collections

Six styles of traps were utilized. The YAW live-catch trap is made of 3-mesh, galvanized hardware cloth with a galvanized sheetmetal door and reinforcement bands. It is 15 inches long by 4½ inches square (Fig. 24). The modified Hubbard trap is made of galvanized sheetmetal, and is 8 inches long and 3 inches square

(Fig. 25). The can pit-trap consists of an outer, galvanized metal case, 7 inches in diameter and 14 inches long, with a stainless steel, flanged inner can of slightly smaller size (Fig. 26). Other

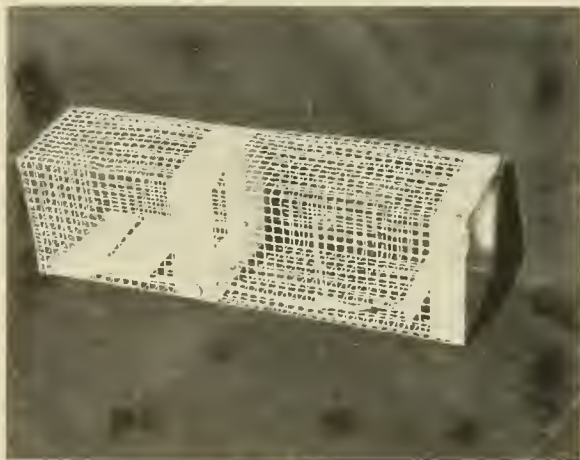


Fig. 24. YAW live-catch trap.

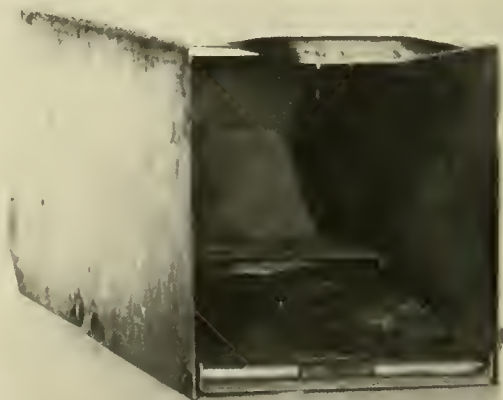


Fig. 25. Modified Hubbard live-catch trap.



Fig. 26. Components of a can pit-trap.

traps used were the Museum Special, break-back trap (Fig. 27) and the Oneida-Victor carnivore trap (Fig. 28). The California gopher trap was used only to a small extent. The YAW, Museum Special, and Hubbard traps were baited with rolled oats, but bait was not used in the other traps. Rifles and shotguns were used to collect rabbits, carnivores, and birds. Reptiles were captured by hand and in can pit-traps. Visual observations of vertebrates were recorded, and many animals found dead along roads and highways were collected.

In each of the 12 primary study areas, traps were arranged in a radiating pattern (Fig. 29). Two traps were placed at each station, with stations approximately 30 feet apart. This same procedure was followed in some cases in the secondary areas, although the traps usually were arranged in single-line transects or randomly



Fig. 28. Oneida-Victor carnivore trap.

placed. Only one can pit-trap was placed at each station, with stations 50 feet apart.

Small mammals found alive in the traps were killed by spinal separation, then put into white paper sacks which were sealed by folding and stapling the tops. Other animals captured alive were killed with chloroform, and these as well as those which were shot were similarly put into paper sacks. All animals returned to the laboratory were refrigerated until further studies could be made. Representative specimens of birds and



Fig. 27. Museum-Special break-back trap.

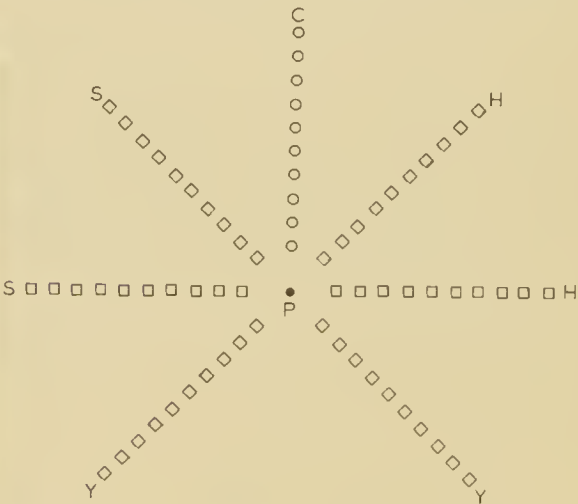


Fig. 29. Trap arrangement used in the major study areas. P, metal post; C, can pit-traps; S, Museum-Special traps; H, Hubbard traps; Y, YAW traps.

mammals were permanently preserved as museum skins, whereas many reptiles were preserved in formalin. Rattlesnakes were taken alive in most cases, examined for ectoparasites, marked for identification purposes, and released. Most of the rabbits, small mammals, and many of the common birds which were damaged were discarded after they were examined for ectoparasites.

During the study period, traps were operated for a total of 57,330 trap nights. Relative to each type of trap, this included 14,040 for YAW, 12,000 for Hubbard, 10,800 for Museum Special, and 20,490 for can pit-traps.

Invertebrate Collections

Most of the ectoparasites were collected by a cooling and warming method. The vertebrate hosts were maintained under normal refrigeration (about 40° F) until their bodies had thoroughly cooled (a few hours to overnight). They were then put into a large, white enamelware pan over which was placed a 100-watt lamp. When the ectoparasites became active and moved away from the cold body of their host, they were retrieved and preserved in vials of 70 percent ethyl alcohol. Additional specimens were obtained by searching through the fur, feathers, or scales of their vertebrate hosts.

Fleas, lice, mites, and some ticks were mounted on microslides for identification purposes, whereas most ticks were retained in alcohol.

Free-living arthropods were collected principally in can pit-traps. Others were taken by modified Berlese funnel extraction (Fig. 30),

some by hand, and others with aerial and beating nets. Many were preserved in 70 percent ethyl alcohol, whereas others were pinned.

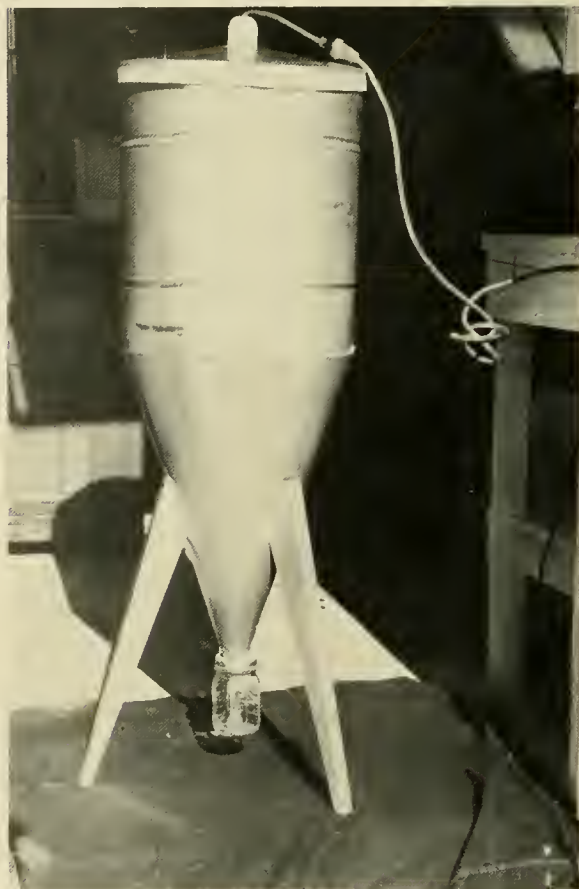


Fig. 30. Berlese funnel.

VERTEBRATES EXAMINED

The kinds and numbers of vertebrates examined for ectoparasites are listed below (also see Table 1). Scientific and common names, number examined, months and areas of collection, and additional comments are listed in sequence, respectively. In most cases the area of collection is listed only when it is one of our 40 specific study sites. Species are listed in alphabetical sequence without regard to phylogenetic relationship in each major category.

Amphibians

Rana pipiens brachycephala (Western Leopard Frog). 1; Aug.; area 28.

Scaphiopus hammondi intermontanus (Great

Basin Spadefoot). 26; June-Aug.; mainly area 6, also in 11, 12. Most taken in July.

Reptiles

Coluber constrictor mormon (Western Yellow-bellied Racer). 1; May; area 24.

Crotalus viridis lutosus (Great Basin Rattlesnake). 95; May-Oct.; areas 3, 19, 20, 24, 36. Most taken from den at area 19 during May, June.

Eumeces skiltonianus utahensis (Western Skink). 5; June, Aug.; area 19.

Masticophis taeniatus taeniatus (Desert Striped Whipsnake). 1; May.

Phrynosoma douglassi douglassi (Pigmy Horned Lizard). 19; April-Sept.; areas 1, 4, 6, 7, 8, 11, 19. Most (11) taken at area 7.

Pituophis catenifer deserticola (Great Basin Gopher Snake). 8; May-Oct.; areas 10, 19, and other.

Sceloporus graciosus (Spiny Lizard). 314; April-Oct.; areas 1, 2, 3, 6, 7, 8, 10, 11, 12, 18. Most collected in June, and from areas 1, 6, 12.

Thamnophis elegans vagrans (Wandering Garter Snake). 3; Oct.; areas 19, 20.

Birds

Acanthis flammea (Common Redpoll). 1; Nov.; area 24.

Actitis macularia (Spotted Sandpiper). 1. July.

Aegolius acadicus (Saw Whet Owl). 2; Sept.

Aeronautes saxatilis (White-throated Swift). 1; June.

Agelaius phoeniceus (Red-winged Blackbird). 1; June; Howe (city).

Aimophila cassinii (Cassin's Sparrow). 2; May; areas 1, 24.

Alectoris graeca (Chukkar). 1; May; area 24.

Amphispiza belli (Sage Sparrow). 38; April-Sept.; areas 1, 2, 7, 10, 11, 23, 24, 25, 29. Most collected in April.

Amphispiza bilineata (Black-throated Sparrow). 1; Aug.; area 7.

Anas discors (Blue-winged Teal). 1; July; area 15.

Anas platyrhynchos (Mallard). 2; Jan., May.

Anthus spinoletta (Water Pipit). 7; April, Oct.; area 23.

Asio flammeus (Short-eared Owl). 4; April, June, Aug., Oct.

Asyndesmus lewis (Lewis' Woodpecker). 2; May.

Bombycilla cedrorum (Cedar Waxwing). 1; Sept.; Atomic City.

Bombycilla garrulus (Bohemian Waxwing). 8; Nov.; area 24.

Bubo virginianus (Great Horned Owl). 1; Nov.

Buteo lagopus (Rough-legged Hawk). 4; Nov., Dec., Jan.

Buteo regalis (Ferruginous Hawk). 2; Aug.; areas 4, 39.

Buteo swainsoni (Swainson's Hawk). 3; April, May, Aug.; Atomic City and other.

Carpodacus mexicanus (House Finch). 2; Nov.; area 20.

Calamospiza melanocorys (Lark Bunting). 4; May, July; areas 7, 24.

Centrocercus urophasianus (Sage Grouse). 18; Feb., May, July, Oct., Nov.; area 24 and other.

Charadrius vociferus (Killdeer). 4; May, Aug.; area 23 and other.

Chordeiles minor (Common Nighthawk). 5; June, Aug.; areas 1, 7, Atomic City and other.

Circus cyaneus (Marsh Hawk). 1; April.

Colaptes cafer (Red-shafted Flicker). 5; May, Sept.; area 24, Atomic City.

Columba livia (Rock Dove). 2; Feb.; Howe (city).

Cyanocitta stelleri (Steller's Jay). 1; Sept.; area 20.

Dendrocopos villosus (Hairy Woodpecker). 1; June; area 24.

Dendroica petechia (Yellow Warbler). 2; May, June; Atomic City and other.

Empidonax difficilis (Western Flycatcher). 3; June.

Empidonax hammondi (Hammond's Flycatcher). 1.

Empidonax oberholseri (Dusky Flycatcher). 1; May; area 24.

Empidonax traillii (Traill's Flycatcher). 1; June; Atomic City.

Eremophila alpestris (Horned Lark). 84; Oct.-Aug.; areas 3, 4, 6, 8, 9, 10, 11, 23, 30, 36. Most birds taken in April, and from area 23.

Ereunetes mauri (Western Sandpiper). 6; May, Aug.; area 19 and other.

Euphagus cyanocephalus (Brewer's Blackbird). 9; April, May; area 23, Atomic City and other.

Falco sparverius (Sparrow Hawk). 6; April, June, Aug., Sept.; area 39 and other.

Hirundo rustica (Barn Swallow). 1; Sept.

Catharus guttatus (Hermit Thrush). 2; May; area 24.

Catharus ustulatus (Swainson's Thrush). 1; June.

Junco oreganus (Oregon Junco). 30; Mar., April, Sept., Oct.; areas 19, 20, 22, 23, 24, 25 and other.

Lanius excubitor (Northern Shrike). 7; Oct., Dec., Jan., Mar.; area 23 and other.

Lanius ludovicianus (Loggerhead Shrike). 20; Mar., April; area 2, Atomic City and other.

Leucosticte tephrocotis (Gray-crowned Rosy Finch). 25; Jan., Feb., Nov.; areas 19, 21, 24 and other.

Loxia curvirostra (Red Crossbill). 3; Nov.; area 24.

Melospiza melodia (Song Sparrow). 1; Mar.; area 3.

Myadestes townsendi (Townsend's Solitaire). 6; Oct.; area 23, 24.

Myiarchus cinerascens (Ash-throated Flycatcher). 1; May.

Nycticorax nycticorax (Black-crowned Night Heron). 1; Aug.; area 15.

Nuttallornis borealis (Olive-sided Flycatcher). 2; May, June; area 2, Howe (city).

Oreoscoptes montanus (Sage Thrasher). 13; April, May, July, Sept.; areas 1, 7, 10, 11, 36 and other.

Parus gambeli (Mountain Chickadee). 2; Sept.; area 20.

Passerina amoena (Lazuli Bunting). 6; May, June; area 24, Atomic City and other.

Perdix perdix (Gray Partridge). 2; Dec.

Petrochelidon pyrrhonota (Cliff Swallow). 3; May, June.

Phasianus colchicus (Ring-necked Pheasant). 5; Jan., Feb., Dec.; Howe (city) and other.

Pica pica (Black-billed Magpie). 8; Jan., Feb., June, Oct., Dec.

Piranga ludoviciana (Western Tanager). 16; May, June; area 24, Atomic City.

Podiceps caspicus (Eared Grebe). 1; May.

Poliophtila caerulea (Blue-gray Gnatcatcher). 1; May.

Poocetes gramineus (Vesper Sparrow). 13; April-Aug.; areas 1, 3, 10, 16 and other.

Recurvirostra americana (American Avocet). 1; July.

Regulus calendula (Ruby-crowned Kinglet). 4; May; area 20 and other.

Regulus satrapa (Golden-crowned Kinglet). 1; Oct.

Salpinctes obsoletus (Rock Wren). 17; May, June, July, Sept., Oct.; areas 19, 20, 24 and other.

Sayornis saya (Say's Phoebe). 2; May, Sept.; areas 19, 23.

Sciurus noveboracensis (Northern Waterthrush). 1; May; area 24.

Selasphorus platycercus (Broad-tailed Hummingbird). 1; June; area 24.

Sialia currucoides (Mountain Bluebird). 5; Mar., April, Sept., Oct.; areas 9, 25 and other.

Spinus pinus (Pine Siskin). 23; Jan., June, Oct., Dec.

Spinus tristis (American Goldfinch). 1; June; Atomic City.

Spizella arborea (Tree Sparrow). 1; Nov.; area 24.

Spizella breweri (Brewer's Sparrow). 7; June, Sept.; areas 2, 24 and other.

Sturnella neglecta (Western Meadowlark). 7; Mar., April, May, July, Sept., Oct.; areas 3, 24 and other.

Sturnus vulgaris (Starling). 9; June, Sept., Oct.; Atomic City and other.

Turdus migratorius (Robin). 11; April, June, Sept.; area 24 and other.

Tyrannus tyrannus (Eastern Kingbird). 3; May, June; area 24 and other.

Wilsonia pusilla (Wilson's Warbler). 3; May, Sept.; area 24 and other.

Zenaidura macroura (Mourning Dove). 23; April-July; areas 2, 24 and other.

Zonotrichia leucophrys (White-crowned Sparrow). 33; May, Sept., Oct.; areas 19, 22, 23 and other.

Mammals

Antilocapra americana (Antelope). 3; April, May, Nov.

Canis latrans (Coyote). 6; Jan., Feb., Aug., Nov., Dec.

Dipodomys ordii (Ord Kangaroo Rat). 808; Mar.-Nov.; all areas except 17, 19-21, 24, 25, 29-32, 34, 35, 38. Mostly in areas 4, 12; seasonally most abundant in Aug.

Erethizon dorsatum (Porcupine). 1; Aug.; area 19.

Eutamias minimus (Least Chipmunk). 398; Mar.-Nov.; all areas except 4, 20, 21, 24, 25, 28-35. Most abundant in areas 1 and 36; most common in July.

Lepus californicus (Black-tailed Jackrabbit). 125; every month except Feb.; areas 5, 10, 13 and other.

Lynx rufus (Wildcat). 8; Jan., Feb., April, Nov.; area 19 and other.

Marmota flaviventris (Yellow-bellied Marmot). 6; May-July; areas 4, 36 and other.

Microtus montanus (Montane Vole). 25; Jan., Mar., June-Aug., Oct., Nov.; areas 1, 3, 15, 27, 30, 38, 39.

Mus musculus (House Mouse). 1; June; area 32.

Mustela frenata (Long-tailed Weasel). 4; July, Aug., Oct.; areas 23, 33, 38 and other.

Myotis evotis (Long-eared Myotis). 2; Mar.; area 20.

Myotis subulatus (Small-footed Myotis). 1; Mar.; area 20.

Neotoma cinerea (Bushy-tailed Woodrat). 14; June-Sept., Nov., Dec.; areas 5, 17, 19, 20, 24, 29, 32, 33.

Onychomys leucogaster (Grasshopper Mouse). 63; Mar.-Dec.; areas 1-3, 7, 9-14, 16, 28, 36, 38. Mostly in area 1.

Ovis aries. (Sheep). 1; July.

Peromyscus maniculatus (White-footed Mouse). 1866; every month; every area. Mostly area 3; most common June-Aug.

Perognathus parvus (Great Basin Pocket Mouse). 474; April-Nov.; all areas except 12, 15, 20-22, 24, 25, 27-35. Mostly areas 1, 2, 7, 10, 36; most common May-Aug.

Plecotus townsendii (Long-eared Bat). 78; Sept.-April; areas 19, 21, 33 and other. Mostly areas 18, 54.

Reithrodontomys megalotis (Harvest Mouse). 39; Mar.-Aug., Oct.; areas 1-3, 7, 10, 11, 13, 15-17, 36, 37. Mostly July, Aug.

Sorex merriami (Merriam's Shrew). 9; April, June-Aug., Oct.; areas 1, 6, 7, 11, 12, 19.

Spermophilus townsendii (Townsend's Ground Squirrel). 60; Mar.-July; areas 1-3, 6-9, 11, 13, 36-38 and other. Mostly June; common areas 3, 9.

Sylvilagus idahoensis (Pygmy Rabbit). 13; Feb., April, June-Aug., Nov.; areas 1-3, 38 and other.

Sylvilagus nuttallii (Nuttall's Cottontail). 28; Feb., Mar., May-Dec.; areas 3, 10, 15, 17, 19-21, 32, 36, 38 and other.

Taxidea taxus (Badger). 5; April-June, Aug., Nov.; areas 30, 37 and other.

Thomomys talpoides (Northern Pocket Gopher). 8; Mar., June, Sept.-Nov.; areas 1, 2, 7, 9, 12, 19, 24.

Vulpes fulva (Red Fox). 4; July; Howe (city).

Table 1. Total number of mammals examined in each study area.

Study area	No. mammals	Study area	No. mammals
1	316	21	59
2	166	22	6
3	561	23	65
4	112	24	5
5	144	25	6
6	165	26	24
7	222	27	9
8	200	28	19
9	139	29	30
10	195	30	14
11	106	31	1
12	165	32	59
13	154	33	24
14	56	34	1
15	88	35	11
16	98	36	349
17	20	37	32
18	53	38	52
19	45	39	35
20	9	40	53

TICKS

Dermacentor andersoni

Hosts

General infestation. Birds of three species and mammals of 16 species were infested (Tables 2 and 3). Only larvae were found on birds. Rodents generally were infested with

larvae and nymphs, whereas adult ticks were found only on rabbits and larger mammals. Exceptions were *Lepus* which possessed larvae, nymphs, and adults; *Sylvilagus* which possessed only nymphs; and a single *Peromyscus* which was host for an adult male tick.

Table 2. Total numbers of ticks collected by species and stage of development.

Species	la	ny	ad ♂	ad ♀	Total
<i>Dermacentor andersoni</i>	3221	542	16	6	3785
<i>Haemaphysalis leporispalustris</i>	73	94	16	10	193
<i>Ixodes kingi</i>	4806	1972	27	66	6871
<i>Ixodes angustus</i> (?)	1				1
<i>Ixodes marmotae</i>	15	1			16
<i>Ixodes ochotonae</i>	25	6			31
<i>Ixodes sculptus</i>			1	3	4
<i>Ixodes</i> sp.	64	4			68

Table 3. Hosts, degree of infestation, and general seasonal occurrence for three developmental stages of *Dermacentor andersoni*.

Host species	% of hosts infested by la, ny, ad	Tick-host index*	Seasonal occurrence
Birds			
<i>Calamospiza melanocorys</i>	la 25 (4)**	1	July
<i>Centrocercus urophasianus</i>	la 6 (18)	1	"
<i>Poocetes gramineus</i>	la 8 (13)	19	"
Mammals			
<i>Dipodomys ordii</i>	la 7 ny 6	4 2	June-Aug. May- "
<i>Eutamias minimus</i>	la 11 ny 11	5 2	June- " May- "
<i>Homo sapiens</i>	ad		June
<i>Lepus californicus</i>	la 3 ny 7 ad 8	1 3 2	Aug. July-Aug. Mar.-April, Aug., Nov.
<i>Lynx rufus</i>	ad 1 (8)	1	April
<i>Microtus montanus</i>	la 8 ny 4	1 1	Aug. July
<i>Mustela frenata</i>	la 25 (4)	1	July
<i>Neotoma cinerea</i>	la 7 (14) ny 29 (14)	10 5	June "-Aug.
<i>Onychomys leucogaster</i>	la 8 ny 13	2 2	July- " June- "
<i>Perognathus parvus</i>	la 15 ny 14	9 2	" - " May- "
<i>Peromyscus maniculatus</i>	la 19 ny 8 ad 0.05	6 2 1	June- " May- " April
<i>Reithrodontomys megalotis</i>	la 8 ny 3	1 1	July-Aug. Aug.
<i>Spermophilus townsendii</i>	la 2 ny 18	2 3	June May-July
<i>Sylvilagus idahoensis</i>	ny 8 (13)	6	Aug.
<i>S. nuttallii</i>	ny 11	1	July, Oct.
<i>Taxidea taxus</i>	ad 20 (5)	1	April

*To nearest whole number.

**Number in parentheses following percentage infested indicates the actual number of hosts examined when less than 20 were collected.

Larvae. Birds were not frequently infested. One larva each was taken from *Calamospiza* and *Centrocercus*, whereas one *Poocetes* possessed 19 larvae.

Of the total mammals examined where large numbers were taken (60 or more), a higher percentage of *Peromyscus* (24%) were infested than were other hosts. The tick-host index (ratio of ticks to number of infested hosts) was highest on *Lepus* and *Perognathus* (10 and 9, respectively). Highest incidence of infestation was 39% for *Perognathus* in August. The highest tick-host index was for *Perognathus* in June (11.6). Average indices on all hosts varied from a low of 5.2 in June to a high of 6.2 in July. There was no proportional correlation between the percentage of animals infested and tick-host index.

Relative to an average of all hosts examined, there was no significant difference between the degree of infestation of male and female hosts. However, the males of *Perognathus* and *Peromyscus* were much more heavily infested than were the females (tick-host index 9.3♂:6.4♀ and 8.2♂:4.7♀, respectively). The opposite situation occurred with *Dipodomys* and *Eutamias* (3.1♂:4.9♀ and 3.7♂:5.9♀, respectively).

Nymphs. Nymphs were found on a greater percentage of *Spermophilus* (26%) than on other hosts. The tick-host index (3) was also highest for this host. The highest incidence of infestation found was for *Spermophilus* (50% infested in August). Highest tick-host index also was related to *Spermophilus*—7.2 in August. Average indices on all hosts varied from a low of 1.0 in October to a high of 2.4 in July. There was no proportional correlation between the percentage of animals infested and the tick-host index.

There was no significant difference between the degree of infestation of males and females for any of the host species.

Adults. Few adults were taken. Thirteen of the 16 males collected were taken from eight *Lepus*, and three of the six females from three *Lepus*.

Seasonal Incidence

Larvae. Ticks of this stage were found only in June, July, and August. Highest percentages of animals were infested in July.

Nymphs. Nymphs were found from May into August; two specimens were taken from *Sylvilagus* (cottontail) in October. Highest percentages of animals were infested in June and August.

Adults. Males were taken in March, April, June, and November, and females in March, April, June, and August.

Haemaphysalis leporispalustris

Hosts

General infestation. Birds of 10 species and mammals of six species were infested (Tables 2 and 4). Only larvae were found on birds with the exception of three Salpinctes which possessed six nymphs. Few rodents were infested, and most mammalian records were for rabbits which possessed larval, nymphal, and adult ticks.

Larvae. Of all birds examined where more than a few were taken (10 or more), a higher percentage of Salpinctes (53%) were infested

Table 4. Hosts, degree of infestation, and general seasonal occurrence for three developmental stages of Haemaphysalis leporispalustris.

Host species	% of hosts infested by la, ny, ad	Tick-host index*	Seasonal occurrence
Birds			
Amphispiza belli	la 5	2	Aug.
Centrocercus urophasianus	la 6 (18)**	1	July
Junco oreganus	la 7	2	Sept.-Oct.
Nuttallornis borealis	la 50 (2)	2	June
Oreoscoptes montanus	la 8 (13)	1	July
Pica pica	la 13 (8)	1	June
Poliopitila caerulea	la 100 (1)	1	May
Salpinctes obsoletus	la 53 (17)	3	May, Sept.-Oct.
	ny 18 (17)	2	Sept.
Selasphorus platycercus	la 100 (1)	1	June
Sturnella neglecta	la 14 (7)	1	July
Mammals			
Lepus californicus	la 10	6	Mar.-Oct.
	ny 16	3	April-Nov.
	ad 23	2	May-Sept.
Onychomys leucogaster	la 2	1	Sept.
Perognathus parvus	la 0.2	1	May
Peromyscus maniculatus	ny 0.2	1	April-June
Sylvilagus idahoensis	la 8 (13)	1	July
	ny 15 (13)	8	June-July
	ad 8 (13)	1	"
S. nuttallii	la 18	3	"- Sept.
	ny 29	9	May-
	ad 18	4	June-July

*To nearest whole number.
**Number in parentheses following percentage infested indicates the actual number of hosts examined when less than 20 were collected.

than were other species. The tick-host index for the birds was highest for Salpinctes (2.6); for other species it was 2.0 or less.

For the mammals, incidence of infestation was highest for Sylvilagus nuttallii (17.8%), although Lepus (which had an infestation rate of 9.6%) had the highest tick-host index, 6.2, as compared with 3.4 for S. nuttallii.

The tick-host index was much higher for male than for female Lepus (14♂:6.4♀) but was not significantly different for other species of hosts.

Nymphs. The only birds possessing nymphs were Salpinctes which had an infestation incidence of 17.6% and a tick-host index of 2.0.

The mammal with the highest incidence of infestation and tick-host index was Sylvilagus nuttallii with 28.6% and 9.4, respectively. One nymph each was found on two Peromyscus; otherwise, most nymphs were found on rabbits.

The tick-host index was much higher for male than for female Sylvilagus nuttallii (15.3♂:6.0♀), but was not significantly different for other species of hosts.

Adults. Adult ticks were found only on rabbits. Highest incidence of infestation was for Lepus (23.2%), but the highest tick-host index was for Sylvilagus nuttallii (4.2).

Only female Sylvilagus nuttallii were infested with adult ticks, whereas both sexes of other hosts were infested.

Seasonal Incidence

Larvae. Larvae were found on birds and mammals from May into October, and one larva was found on a mammal in March. Insufficient numbers were taken to determine the month of highest incidence.

Nymphs. Nymphs were found on birds in September, and on mammals from April into November. Highest incidence apparently was June into August.

Adults. Males were taken from May into September, and females from May into July. Highest incidence was from June into August.

Ixodes kingi

Hosts

General infestation. Mammals of 11 species were infested (Tables 2 and 5). Principal hosts for these ticks are Onychomys, Dipodomys, Perognathus, and Peromyscus.

Larvae. The highest incidence of infestation occurred with Onychomys. Dipodomys

Table 5. Hosts, degree of infestation, and general seasonal occurrence for three developmental stages of *Ixodes kingi*.

Host species	% of hosts infested by la, ny, ad	Tick-host index*	Seasonal occurrence
Mammals			
<i>Dipodomys ordii</i>	la 22 ny 40 ad 5	13 4 1	Mar.-Nov. " - " " - Oct.
<i>Eutamias minimus</i>	la 4 ny 1 ad 0.2	1 1 1	Mar., June-July, Oct. Mar., June-July June
<i>Lepus californicus</i>	la 2	1	April
<i>Microtus montanus</i>	ny 4	1	Aug.
<i>Mustela frenata</i>	la 0.8 ny 1 ad 2	3 8 5	July-Oct. " - " " - "
<i>Neotoma cinerea</i>	la 14 (14)** ny 36 (14)	6 6	June-Aug. " - Sept.
<i>Onychomys leucogaster</i>	la 46 ny 22 ad 2	9 4 2	Mar., June-Dec. June-Oct. July
<i>Perognathus parvus</i>	la 12 ny 14 ad 0.4	4 2 1	May-Oct. " - " July
<i>Peromyscus maniculatus</i>	la 10 ny 5 ad 0.05	6 3 1	Jan.-Dec. " - Oct. March
<i>Spermophilus townsendii</i>	la 5 ny 7	23 8	Mar., June " - "
<i>Taxidea taxus</i>	ny 20 (5) ad 60 (5)	1 2	Aug. April, Nov.
<i>Thomomys talpoides</i>	la 13 (8) ny 13 (8)	14 12	June "

*To nearest whole number.

**Number in parentheses following percentage infested indicates the actual number of hosts examined when less than 20 were collected.

were about one-half, and *Perognathus* and *Peromyscus* were about one fourth as frequently infested. The average tick-host index for *Dipodomys* (11.2) was about twice that for other hosts.

The tick-host index was not significantly different for males and females of host species except for *Onychomys* wherein the index for females was 50% higher than for males (6.1♂: 4.5♀).

Nymphs. The highest incidence of infestation occurred with *Dipodomys*. The tick-host index for *Onychomys* was about two times higher than for *Perognathus* and *Peromyscus*, but was only slightly higher than *Dipodomys*.

The tick-host index was not significantly different for males and females of host species except for *Onychomys* wherein the index for males was almost three times higher than for females (7.5♂:2.8♀).

Adults. Although adults were taken from a variety of hosts, most were infrequent infestations. The average incidence on *Dipodomys* was about 4%, whereas for *Mustela* and *Taxidea* it was almost 100%. The average tick-host index was five on *Mustela* as compared to about two for other hosts.

Seasonal Incidence

Larvae. Larvae were found every month except February. Peak populations occurred in March, June, and October. Few specimens were taken in January, September, November, and December.

Nymphs. Ticks of this stage were found every month except February and December. Only one nymph was taken in January, and five in November. Highest incidence occurred in March, June, and October.

Adults. Males were taken from March into October, except in May and September, and predominantly in July and October. Females were taken from March into October, also predominantly in July and October.

Other Species

Ixodes angustus

One larva was taken from a male *Spermophilus* in June.

Ixodes marmotae

Four larvae were taken from a male *Marmota* in May, and 11 larvae from a male *Marmota* in June. One nymph was taken from a female *Spermophilus* in June.

Ixodes ochotonae

Twenty-five larvae were taken from a female *Spermophilus* in June. Two nymphs were taken from a male *Neotoma* in August, and four from a female in September.

Ixodes sculpus

One male and three female ticks were taken from a male *Taxidea* in August.

Ixodes sp.

A number of *Ixodes*, mostly larvae, unidentifiable to species, were taken from the following hosts:

- Agelaius phoeniceus*, one larva in June from a male bird.

Dendrocopos villosus, 17 larvae in June from a female bird.

Lanius ludovicianus, three larvae and one nymph in April.
- Passerina amoena*, one nymph in May from a male bird.

Microtus montanus, two nymphs in June.

Reithrodontomys megalotis, four larvae in March from a female mouse.

Spermophilus townsendii, one larva in March, one in April, and 37 in June.

DISCUSSION

Trapping Efficiency

For the past 17 years during ecological studies in the cold deserts of western North America, my associates and I have used several kinds of animal traps and bait with various degrees of success. Live-catch traps have captured more of the small nocturnal rodents than other traps, and in the Idaho study this also was the case. The live-catch traps caught up to four times as many animals as the break-back type. The YAW trap was twice as efficient as the Hubbard trap for harvest mice, white-footed mice, pocket mice, and kangaroo rats (nocturnal species). The YAW and Hubbard traps demonstrated about equal efficiency for ground squirrels and chipmunks (diurnal species). However, three times as many grasshopper mice (nocturnal) were caught in the Hubbard traps compared to the YAW traps. These relative efficiencies likely are related to bait retention, conspicuousness of the trap, and retention of animal odors which may be attractive to some species and repulsive to others.

The can pit-trap, efficient for some amphibians, reptiles and ground-dwelling arthropods, occasionally captured rodents. However, the numbers caught are insignificant except for *Sorex* and *Microtus* which were frequently caught in the cans. Nuttall's and pygmy cottontail rabbits occasionally were found in YAW

traps. Ground-dwelling birds, such as the Vesper Sparrow, Sage Thrasher, Horned Lark, and Sage Sparrow, were caught infrequently in the YAW and break-back traps.

Interaction of Tick Species

It is assumed that competition occurs between ticks of different species relative to their simultaneous infestation of the same host. This was not the situation, however, for *Dermacentor* and *Ixodes* (Table 6). In most cases the percentage of animals infested with ticks of both species simultaneously was higher than expected as demonstrated particularly on *Perognathus*. *Onychomys* demonstrated the expected pattern, and fewer animals were infested with both ticks than was expected.

Other species combinations seldom occurred, although this may have been due to the fewer numbers of ticks collected. No *Lepus* was taken on which only *Dermacentor* was found, but 30% of these hosts were infested only with *Haemaphysalis*; eighteen percent were infested with both *Dermacentor* and *Haemaphysalis*. Only four hosts, each of a different species, were infested with different species of *Ixodes* simultaneously. Seven other hosts representing four species possessed ticks of different genera simultaneously.

Table 6. Interaction relative to occurrence of *Dermacentor andersoni* and *Ixodes kingi* on common hosts.

Host and sample size	Actual % of hosts infested with			Expected % infestation with both ticks
	Only <i>D. andersoni</i>	Only <i>I. kingi</i>	Both ticks	
<i>Dipodomys ordii</i> (808)	8	63	5	5
<i>Eutamias minimus</i> (398)	2	4	0.5	0.08
<i>Lepus californicus</i> (125)	18	2	0.8	0.4
<i>Onychomys leucogaster</i> (63)	14	64	6	8.9
<i>Perognathus parvus</i> (474)	22	14	13	3
<i>Peromyscus maniculatus</i> (1866)	22	11	5	2.4
<i>Spermophilus townsendii</i> (60)	15	7	5	1

Ecological Distribution of Ticks

Insufficient detailed analyses of the habitats were made to correlate the occurrence of ticks with both soil and plant types. However, the frequency of occurrence of *Dermacentor* and *Ixodes* ticks was greatest in the sage-grass associations and around reservoirs (Tables 7 and 8). Where grass and sage were present in only small amounts, or where either occurred in abundance with plants of other species, ticks were not as abundant. Ticks were conspicuously absent in the grassy, sinks area of site 15. Although mammals occur there in moderate numbers (Table 1), the periodic, spring flooding of this lowland area may be effective in eliminating the unattached ticks which normally await the passing of a suitable host.

In at least six areas where *Dermacentor* and *Ixodes* occurred simultaneously, a significant difference between their frequency indices was

Table 7. Frequency index of occurrence¹ of *Dermacentor* and *Ixodes* in selected study areas².

Study area	<i>Dermacentor</i>	<i>Ixodes</i>
1	.08	.05
2	.008	.003
3	.24	.03
4	°	.05
5	.02	.15
6	.005	.03
7	.02	.04
8	.18	.05
9	.001	.06
10	.02	.04
11	.003	.07
12	.001	.23
13	.17	.08
14	0	°
15	0	0
16	.03	.08
18	°	.04
23	°	.91
29	°	0
32	.01	.14
36	.75	1.0
38	1.0	.34
40	.76	.17

¹Relative to the highest populations found (in area 36 for *Ixodes* and area 38 for *Dermacentor*) indicated as 1.0.

²Areas where an adequate sample of mammals and the principal hosts were examined during the known seasonal occurrence of the species of ticks.

°Not applicable for reasons stated in footnote 2.

noted (Table 7). In areas 3, 38 and 40, *Dermacentor* was greatly predominant, whereas in areas 12, 23 and 36, *Ixodes* was predominant. In seven of 21 areas *Dermacentor* was slightly more abundant than *Ixodes*, whereas in 13 areas *Ixodes* was the more abundant.

Table 8. Frequency index¹ of ticks in representative plant community types and areas.

Predominant plant type or area	Frequency index	
	<i>Dermacentor</i>	<i>Ixodes</i>
Grass	.03	.145
Juniper	.02	.15
Sage	.39	.1
Sage-Grass	.87	.67
Sage-Grass-Juniper	.001	.23
Sage-Rabbitbrush	.029	.058
Sage-Saltbush	.18	.05
Rabbitbrush-Grass	.003	.07
Rabbitbrush-Horsebrush	.005	.03
Goosefoot-Winterfat	.001	.06
Sand Dunes (shifting and semi-permanent)	0	.04
Reservoirs (semi-permanent)	0	.91

¹Average taken between all areas of the specific plant type, so highest index possible will not equal 1.0. Refer to footnote 1 of Table 7.

Radiation Effects

Although the evidence relating to the effects of low-level radiation on parasites and their hosts is circumstantial and available for only one area, it is sufficient to warrant further detailed studies. In an area where radioactive wastes were buried, fewer ticks and infested mammals were found than in a non-irradiated control area of a similar habitat. At study 13 (radioactive waste burial ground near NRTS facility EBR-1) the frequency index was lower for *Dermacentor* and *Ixodes* than at the non-irradiated control site (area 38) 0.3 mile away (Table 9). Similarly, the tick-host index was much lower in the irradiated area than at the control site.

Table 9. Relative infestation and abundance of ticks in irradiated and non-irradiated control areas.

Factor	Irradiated area		Non-irradiated area	
	<i>Dermacentor</i>	<i>Ixodes</i>	<i>Dermacentor</i>	<i>Ixodes</i>
Frequency index	.17	.08	1.0	.34
Tick-host index	.93	.67	5.4	2.72

SUMMARY

During the period from June, 1966, to September, 1967, 27 amphibians of two species, 446 reptiles of eight species, 561 birds of 81 species, and 4050 mammals of 26 species were examined for ectoparasites at the National Reactor Testing Station in southern Idaho. Of seven species of ticks collected, the predominant one was *Ixodes kingi*, found on mammals of 12 species. Next in abundance was *Dermacentor andersoni* found on birds of three species and mammals of 16 species. *Haemaphysalis leporispalustris* was taken from birds of 10 species and six species of mammals. Four other species of *Ixodes* were taken from birds of four species and seven species of mammals.

Where adequate samples were taken, the highest percentage of hosts infested with *Dermacentor andersoni* was 8% for birds and 29% for mammals. *Haemaphysalis leporispalustris* was found on as many as 53% of the birds and 29% of the mammals. *Ixodes kingi* infested as many as 46% of the mammals.

Apparently there was little competition between ticks of different species relative to their simultaneous infestation of the same host.

Highest populations of ticks were found in areas where both sagebrush and grass were predominant. In one irradiated area the rate of infestation and population of ticks were significantly lower than in an adjacent, non-irradiated control area.

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**NEW RECORDS AND SPECIES OF
NEOTROPICAL BARK BEETLES
(SCOLYTIDAE: COLEOPTERA)
PART IV**

by
STEPHEN L. WOOD



BIOLOGICAL SERIES — VOLUME X, NUMBER 2

JUNE 1969

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**Brigham Young University
Science Bulletin**

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NEOTROPICAL BARK BEETLES
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PART IV**

by
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NEW RECORDS AND SPECIES OF NEOTROPICAL
BARK BEETLES (SCOLYTIDAE: COLEOPTERA)
PART IV¹

BY

Stephen L. Wood²

On the following pages 108 species and two subspecies of bark beetles (Scolytidae) are described as new to science. It was intended that most of these would be named in a synopsis of the Scolytidae of Costa Rica; however, the volume of undescribed material proved to be so large and the manuscript treating it so bulky that its completion became impractical. That manuscript, with its keys, host and geographical distributions, and biological notes is being expanded into a treatment of the entire American continent north of Panama. In order to stabilize new names for that project, they are validated below.

The new species represent the following genera: *Xylechinus* (1), *Phrixosoma* (1), *Phloeosinus* (1), *Chramesus* (8), *Phloeotribus* (5), *Chaetophloeus* (1), *Liparthrum* (2), *Cnemonyx* (5), *Camptocerus* (1), *Scolytus* (2), *Microborus* (2), *Scolytodes* (22 with 2 subspecies), *Pseudothyssanoes* (16), *Cryptulocleptus* (13), *Thysanoes* (4), *Micracisella* (8), *Micracis* (9), *Hylocurus* (4), *Phloeocleptus* (3). They are from the following countries: Mexico (49), Guatemala (9), Honduras (7), Costa Rica (49), Panama (5); seven species occurred in two countries, and two species occurred in three countries.

Except as noted below, all type series were tentatively deposited in my personal collection presently housed at the Brigham Young University, in order to facilitate preparation of a monograph of the Scolytidae of the western hemisphere. Upon conclusion of that monograph, paratypes will be distributed, in so far as possible, to at least two European and two other American collections. The British Museum (Natural History) has already received paratypes of many species.

Xylechinus avarus, n. sp.

The large body size, the stout form, the elevated declivital interspaces 1 and 3 on the elytra, the fine ground vestiture, and the fine, low frontal carina serve to distinguish this species. Of the species known to me it is perhaps more closely allied to *fuliginosus* Blandford, although the relationship is remote.

Female.—Length 3.2 mm. (paratypes 2.4–3.3 mm.), 2.1 times as long as wide; body color brown, usually covered by an incrustation.

Frons convex, with a feeble transverse impression

just below upper level of eyes, a low acutely elevated median carina extending from this impression to epistomal margin; entire surface coarsely reticulate, punctures fine, inconspicuous; vestiture short sparse inconspicuous.

Pronotum 0.93 times as long as wide; sides widest and almost parallel on middle half, strongly constricted one-fourth length from anterior margin, rather broadly rounded in front; surface finely granulate and with rather sparse, round, small vulcanate punctures; vestiture consisting of short, rather stout, moderately abundant bristles.

Elytra 1.2 times as long as wide, 1.8 times as long as pronotum; sides almost straight, very slightly wider at declivital base, narrowly rounded behind; striae impressed, the punctures deeply, not sharply impressed; interstriae about one and one-half times as wide as striae, irregular, the punctures fine, abundant, confused, with a median row of larger, granulate punctures, crenulate toward base. Declivity convex, rather steep; striae impressed; interspace 2 impressed, strongly narrowed, ending before apex, 1, 3, and 9 elevated, about half as high as wide, 3 and 9 join apically, the elevation continued to 1, granules not as large as on disc. Vestiture of short, rather abundant, stout, hairlike setae, and interspatial rows of long bristles, spacing between bristles and between rows equal to length of a bristle.

Male.—Similar to female except frons flattened on lower half; and ground vestiture evidently more abundant.

Type Locality.—Volcan Irazu, Cartago Prov., Costa Rica.

Host.—*Oreopanax nubigenus*.

Type Material.—The male holotype, female allotype, and 205 paratypes were collected at the type locality on October 26, 1963, at an elevation of 2,300 m., by S. L. Wood, from the fallen epiphytic host that was about 10 cm. in diameter. The galleries were similar to those of *fuliginosus*. The holotype, allotype and paratype are in my collection.

Phrixosoma clusiae, n. sp.

This species is very closely related to *minor* Wood, but it may be distinguished by the larger size, by the much more strongly impressed female vertex, by having the interstitial granules three-ranked almost to elytral base, by the comparatively wider discal interstriae, and by the less definitely granulate anterior slope of the pronotum.

Female.—Length 2.5 mm. (paratypes 1.9–2.5 mm.), 1.9 times as long as wide; color black.

Frons broadly convex from epistomal margin to upper level of eyes; rather strongly, transversely, arcuately impressed from just above level of eyes to vertex, upper margin of this groove abruptly angled; lateral angles of groove produced laterally causing a pro-

¹Part of the field work that led to the discovery of these insects was sponsored by the National Science Foundation.

²Department of Zoology and Entomology, Brigham Young University, Provo, Utah. Scolytoidea contribution number 38.

nounced situation in line where pubescent and non-pubescent areas meet; vestiture hairlike, short, rather abundant, extending to vertex.

Pronotum 0.80 times as long as wide; widest at base, sides uniformly, convergently arcuate to weak constriction just before the rather narrowly rounded anterior margin; anterior third very minutely asperate, asperities on margin somewhat larger; surface rather closely marked by low, subreticulate, short, irregular rugae (remnants of interspaces between obsolete punctures), depressed areas reticulate; vestiture consisting of very fine, short hair.

Elytra 1.2 times as long as wide, 1.7 times as long as pronotum; outline as in *obesa*; narrowly impressed, the punctures small, distinct; interstriae almost three times as wide as striae, reticulate, granules rather large, rounded, three-ranked almost to base except on 2, the marginal rows of granules becoming smaller by middle of disc and obsolete by upper fourth of declivity. Declivity and vestiture as in *minor*.

Male.—Similar to female except frontal carina absent, vertex and anterior margin of pronotum not modified, and asperities on anterior third of pronotum almost obsolete.

Type Locality.—Zamorano, Morazan, Honduras.

Host.—*Clusia flava*.

Type Material.—The female holotype, male allotype, and ten paratypes were collected at the type locality on April 18, 1964, 700 m. elevation, No. 561, in branches and bole of *Clusia flava*. This monogamous species constructs biramous, transverse egg galleries in the cambium region essentially as in *minor*.

The holotype, allotype, and paratypes are in my collection.

Phloeosinus palearis, n. sp.

This species is closely allied to *serratus* LeConte, but it may be distinguished by the smaller size, by the numerous minute points and/or fine lines in the interspaces between punctures on the pronotal disc, by the less numerous, smaller submarginal crenulations at the elytral bases, and by the less strongly compressed teeth on the male elytral declivity, the anterior profile of each tooth usually evenly arcuate (abruptly angled in *serratus*).

Male.—Length 2.4 mm. (paratypes 1.9-2.5 mm.), 1.95 times as long as wide; color very dark brown.

Frons feebly convex, almost flat, the lower fourth gradually ascending to epistomal margin; lower half marked by a fine, low median carina; surface smooth with rather line, deep, close punctures, some subgranulate in area median to upper half of eye; vestiture fine, moderately long, rather abundant. Vestiture on antennal club short, more abundant than in allied species.

Pronotum 0.82 times as long as wide; widest near base, the sides strongly, convergently arcuate to moderate constriction just before broadly rounded anterior margin; surface smooth, with some minute points and lines in interspaces between the moderately large deep punctures; interspaces one-fourth to equal in width to

diameter of a puncture. Vestiture fine, rather short, moderately abundant.

Elytra 1.2 times as long as wide, 1.6 times as long as pronotum; basal margins armed by 12 crenulations on interstriae 2-9; striae narrowly impressed, the small punctures somewhat obscurely indicated; interstriae about three times as wide as striae, feebly convex, the surface smooth but irregular, the punctures moderately coarse, close, confused, their anterior margins usually elevated, some rather coarsely crenulate at base. Declivity convex, rather steep; striae less strongly impressed; interstriae 1 and 3 moderately, 5, 7, 8 less strongly elevated, these and 6 armed by rather coarse teeth, those on 3 and particularly on 1 larger, 2 bearing two teeth near apex, 2 and 4 flat, finely punctured; interstriae 1 bearing eight teeth, each only slightly compressed and usually with anterior profile evenly arcuate, 3 bearing 13 teeth with none of them compressed. Vestiture scanty, but stout, some setae almost scalelike.

Female.—Similar to male except frons more strongly convex and more extensively granulate; pronotal lines and points much more abundant; a few elytral crenulations extend almost to declivity; declivital teeth smaller with interstriae 2 and 4 armed by at least a few small teeth; declivital vestiture largely of scales each only slightly longer than wide.

Type Locality.—Sixteen km. east Chiapa de Corzo, Chiapas, Mexico.

Host.—*Juniperus* sp.

Type Material.—The male holotype, female allotype, and 13 paratypes were collected at the type locality on June 17, 1964, at an elevation of about 2,300 m., No. 710, from a small *Juniperus* branch.

The holotype, allotype and paratypes are in my collection.

Chramesus gracilis, n. sp.

This species is in the subgenus *Prochramesus* and is allied to *annectans* Wood, but may be distinguished by the larger size, by the much more finely, shallowly punctured pronotum, by the smaller, shallow striae punctures, and by other characters.

Male.—Length 2.5 mm. (paratypes 2.2-2.7 mm.), 2.25 times as long as wide; color dark brown to black, with white vestiture.

Frons rather deeply, concavely impressed from upper level of eyes to epistoma, the lateral margins rounded, bearing mesad of margin just above antennal bases, a pair of large squared processes as in *annectans*; surface coarsely reticulate with a few fine, obscure punctures; vestiture fine, long, rather sparse. Antennal club acutely pointed.

Pronotum 0.9 times as long as wide; widest at base, sides weakly arcuate and converging slightly on basal two-thirds then rather strongly constricted before the broadly rounded anterior margin; surface reticulate, with fine, rather widely separated punctures, the punctures indistinctly vulcanate or subasperate in lateral areas; vestiture consisting of stout semirecumbent bristles.

Elytra 1.5 times as long as wide, 1.9 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind, striae not im-

pressed, the punctures small, round, shallow, distinct; interstriae about three times as wide as striae, almost flat, smooth and shining with rather abundant, minute, setiferous, confused punctures and median rows of fine setiferous granules. Declivity steep, convex; striae weakly impressed, the interspaces feebly convex. Vestiture consisting of rather abundant, short, subplumose scales and interstitial rows of somewhat longer erect bristles, each bristle about two-thirds as long as distance between rows.

Female.—Similar to male except frons very shallowly impressed, the tubercles somewhat smaller; pronotal tubercles distinctly larger.

Type Locality.—University of Costa Rica Campus, San José, Costa Rica.

Host.—*Bambusa vulgaris*.

Type Material.—The male holotype, female allotype, and 83 paratypes were collected at the type locality on September 12, 1963, at an elevation of about 1,300 m., by S. L. Wood, from dead and dying stumps of Japanese bamboo which were 10 cm. or more in diameter. The diagonal, biramous, egg galleries were just under the surface of the wood. Larval mines were parallel to the grain of the wood.

The holotype, allotype, and paratypes are in my collection.

Chramesus ingens, n. sp.

Among the species known to me this one is unique in having the antennal bases comparatively close together and higher than usual; in having the elytral vestiture fine and of uniform length; and in having the male frons not excavated, but the lateral margins elevated with the raised tubercle at a point well above the antennal insertion.

Male.—Length 2.7 mm. (paratypes 2.4–2.8 mm.), 1.6 times as long as wide; color dark brown or black.

Frons impressed from upper level of eyes to epistoma with a low elevation between antennal bases, lateral margins elevated on middle third with a rounded tubercle just above antennal base; surface reticulate, with very fine punctures at sides and above; antennal bases closer together than eyes, distance from epistomal margin (omitting lobe) to antennal bases 1.6 times greatest width of eye; frons subglabrous. Antennal scape with small tuft of hair.

Pronotum 0.8 times as long as wide; base strongly bisinuate, basal angles broadly rounded, sides strongly arcuate, widest just behind middle, moderately constricted just behind the broadly rounded anterior margin; entire surface reticulate and with small, sparse, finely subasperate punctures, finer in posteromedian area; glabrous.

Elytra 1.03 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on basal half, broadly rounded behind; striae narrowly impressed, the punctures small, distinctly impressed; interstriae about three times as wide as striae, slightly convex almost smooth with numerous, confused, small rounded setiferous granules. Declivity convex, moderately steep; about as on disc. Vestiture consisting of fine, erect, confused, hairlike setae, all of equal length, each shorter than a distance equal to width of an interspace (about

two-thirds as long).

Female.—Similar to male except frontal margin feebly elevated and not armed; pronotal punctures almost entirely devoid of small asperities.

Type Locality.—Tapanti, Cartago Prov., Costa Rica.

Host.—*Serjania mexicana*? (probable error in identification).

Type Material.—The male holotype, female allotype, and 270 paratypes were collected at the type locality on October 24, 1963, at an elevation of about 1,300 m., by S. L. Wood, from a vine having three leaflets per leaf. The host was identified as *Serjania mexicana*, however, the tissues were very moist, soft and non-woody and turned black with age, suggesting an error in identification. This species was also collected at Puerto Viejo, Heredia Prov., and at Guapiles, Limon Prov., in humid lowland areas, but these specimens were not included in the type series.

The holotype, allotype, and paratypes are in my collection.

Chramesus acacicolens, n. sp.

Similar to *crenatus* Wood, but distinguished by the deeper, wider stria punctures, by the much shorter, wider, erect interstitial scales, by the small tubercles of elytral interspaces, and by other characters.

Male.—Length 1.8 mm. (paratypes 1.5–1.8 mm.), 1.65 times as long as wide; color light brown.

Frons broadly, concavely excavated from upper level of eyes to epistoma, deepest point near middle, subfoveate; lateral margins acute below, armed by a pair of tubercles just below level of antennal insertion; surface coarsely reticulate, a few minute punctures scarcely visible; vestiture short, inconspicuous.

Pronotum 0.73 times as long as wide; median basal area produced slightly into scutellar notch, sides widest near base, rather strongly arcuate, constricted just behind the broadly rounded anterior margin; surface minutely rugulose, dull, rather finely, shallowly punctured, the punctures becoming finely asperate toward anterior and lateral areas; vestiture consisting of short, stout bristles.

Elytra 1.07 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal half, broadly rounded behind; striae impressed, the punctures rather large and deep; interstriae about twice as wide as striae, convex, with small, abundant, squamiferous punctures and median rows of tubercles that decrease in size posteriorly. Declivity convex, moderately steep; as on disc except tubercles not evident. Vestiture consisting of abundant short scales and interstitial rows of erect scales slightly more than twice as long as ground vestiture, each large scale about three times as long as wide.

Female.—Similar to male except frons weakly convex, transversely impressed just above epistoma, minute punctures more evident; pronotal asperities evident only at anterolateral angles.

Type Locality.—Finca La Pacifica, 4 km.

northwest of Cañas, Guanacaste Prov., Costa Rica.

Host.—*Acacia* sp.

Type Material.—The male holotype, female allotype, and 80 paratypes were collected at the type locality on July 13, 1966, at an elevation of 50 m., by S. L. Wood, from the cambium region of branches and twigs of the host tree less than 2 cm. in diameter.

The holotype, allotype, and paratypes are in my collection.

Chramesus varius, n. sp.

This is the only species of *Chramesus* known to me in which the frons is concave in both sexes and the epistoma is armed in both sexes by a large median tubercle; the variegated color pattern of the scales is also unique in the genus.

Male.—Length 1.5 mm. (paratypes 1.4-1.7 mm.) 1.7 times as long as wide; color brown with light colored scales on basal fourth and lateral margins of pronotum and on interstriae 1 and lateral areas of elytral disc, dark scales predominate elsewhere.

Frons deeply, broadly, concave from eye to eye from well above eyes to epistoma; excavated area reticulate-granulate; lateral margin acute only at level of antennal bases, unarmed; epistomal margin bearing a large, pointed, median tubercle; vestiture consisting of moderately abundant, stout setae. Scape bearing a conspicuous tuft of long, yellow, subplumose setae; club rather small for this genus, its apex not pointed.

Pronotum 0.82 times as long as wide; widest on basal third, the sides strongly, convergently arcuate toward the broadly rounded anterior margin; anterolateral areas with a few fine asperities; surface coarsely reticulate, the punctures rather fine, shallow, moderately close, many of them subvulcanate on posterior area; basal margin bisinuate; vestiture stout, short, essentially scalelike.

Elytra 1.14 times as long as wide, 1.6 times as long as pronotum; bases armed by 11 marginal crenulations on interstriae 2-9; scutellum not visible in usual sense; striae weakly impressed, stronger toward declivity, the punctures small, impressed; interstriae twice as wide as striae, convex, the surface evidently superficially reticulate, the punctures very fine, usually obscured by setae. Declivity convex steep; striae slightly deeper, interstriae slightly narrower than on disc. Vestiture consisting of moderately abundant, stout, almost scalelike, erect setae, and rows of erect scales each about twice as long as ground vestiture and about four or five times as long as wide.

Female.—Similar to male except frons more narrowly, shallowly concave with median tubercle a little smaller; pronotal crenulations larger and more numerous.

Type Locality.—Twenty-seven km. north of Ixmiquilpan, Hidalgo, Mexico.

Host.—*Acacia* sp.

Type Material.—The male holotype, female allotype, and 12 paratypes were collected at the type locality on July 10, 1967, elevation 1,900 m., No. 188, in an *Acacia* branch about 4 cm. in

diameter, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Chramesus secus, n. sp.

This species is exceedingly similar to *varius* Wood, described above, but differs by the larger size, by the uniformly light color of the vestiture, by the more finely sculptured pronotum, and by the shorter, more scalelike vestiture. This possibly could be a subspecies of *varius*.

Male.—Length 1.7 mm., 1.7 times as long as wide; color brown with white vestiture on pronotum and interstriae 1, tan elsewhere.

Exactly as in *varius* except as noted above and also setae on all margins of pronotum shorter and stouter; median extension of basal margin of pronotum less pronounced; elytral vestiture appearing more abundant and each seta conspicuously wider.

Type Locality.—Laguna Santa Maria, Nayarit, Mexico.

Type Material.—The unique male holotype was taken with a series of the following species on July 6, 1965, near 1,000 m. elevation, No. 201, by S. L. Wood. The host was a large woody vine (liana) having the larger stems square in cross section.

The holotype is in my collection.

Chramesus unicornis, n. sp.

This species is rather closely allied to *varius* Wood, described above, but it is easily distinguished by the less extensive male frontal impression, by the smaller tuft of setae on the scape, by the subquadrate pronotum, by the more strongly impressed striae and striae punctures, and by the uniformly light colored vestiture.

Male.—Length 1.4 mm. (paratypes 1.3-1.6 mm.), 2.0 times as long as wide, color medium to light brown.

Frons deeply excavated from eye to eye from upper level of eyes to epistoma; lateral margins acute from just above level of antennal insertion to epistomal margin; surface rather coarsely reticulate above, becoming obscurely reticulate and shining below, armed by a large, pointed, median tubercle immediately above epistomal margin; vestiture sparse, inconspicuous. Antennal scape bearing a small tuft of fewer than a dozen long, yellow setae; club small for this genus.

Pronotum 0.83 times as long as wide; widest at base, the sides feebly arcuate and converging slightly on more than basal two-thirds, then rather abruptly constricted just before the broadly rounded anterior margin; surface rather coarsely reticulate, the punctures very close, rather shallow, irregular in outline, anterolateral asperities obscure. Vestiture consisting of short, rather abundant, stout, almost scalelike setae.

Elytra 1.2 times as long as wide, 1.5 times as long as pronotum; sides straight and subparallel on basal two-thirds to declivital base, then rather broadly rounded behind; basal margins armed by 14 crenulations; striae slightly impressed, the large punctures deeply impressed; interstriae as wide as striae, convex, each bearing a

row of fine, pointed tubercles. Declivity moderately steep, convex, essentially as on disc except area at junction of interstriae 3 and 9 slightly elevated. Vestiture consisting of moderately abundant, small, broad scales, and rows of erect interstitial scales about three times as long as ground cover, each half as long as distance between rows and almost equal in length to distance between erect scales within a row, about four times as long as wide; not longer on declivity.

Female.—Similar to male except frons convex, coarsely reticulate to epistoma, the median tubercle absent and pronotal asperities slightly larger.

Type Locality.—Laguna Santa María, Nayarit, Mexico.

Type Material.—The male holotype, female allotype, and 76 paratypes were collected at the type locality on July 6, 1965, about 1,000 m. elevation, No. 201, from the phloem tissues of the host, by S. L. Wood. The host was a large woody vine (liana) about 7 cm. in diameter, having the cross-section of the larger stems square. Four paratypes were taken 25 km. west of Armaria, Colima, Mexico, on June 30, 1965, No. 143, from the same host, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Chramesus cecropiae, n. sp.

In this unique species the male frons is not excavated, but more nearly protuberant at a level just above the antennal bases; in addition, the elytral ground vestiture is totally absent, a row of stout bristles marks each interstriae.

Male.—Length 1.25 mm. (paratypes 1.3 mm.), 1.7 times as long as wide; color rather dark brown, the elytra somewhat lighter.

Frons longitudinally flattened, transversely, weakly convex on upper third, then ascending rather abruptly below to an indefinite, strongly arcuate line between antennal bases, its median point well above (dorsad) its lateral extremities; lower two-thirds almost flat, the lateral margins below very slightly elevated; surface above coarsely reticulate, lower area transversely strigose; vestiture consisting of a few hairlike setae on lateral areas on lower half. Antennal club moderately large for the genus.

Pronotum 0.82 times as long as wide; widest on basal third, sides arcuately converging to a slight constriction just before the rather broadly rounded anterior margin; surface shining, subreticulate, with scattered, rather abundant tubercles of variable size on anterior three-fourths, some of those on anterolateral area finely asperate; a few large, obscure punctures evident toward base. Vestiture rather sparse, consisting of a few stout setae over entire surface.

Elytra 1.1 times as long as wide, 1.4 times as long as pronotum; elytral bases armed by about 12 crenulations; striae feebly if at all impressed, the punctures large, moderately deep, distinct; interstriae very slightly wider than striae, very slightly irregular, brightly shining, each bearing a row of small, pointed, setiferous tubercles. Declivity rather steep, convex, sculptured essentially as on disc. Vestiture consisting of rows of interstitial bristles, each bristle somewhat flattened toward its apex

and equal in length to distances between bristles within and between rows; very minute striaal hairs also evident.

Female.—Similar to male except frons more evenly convex, coarsely reticulate throughout, with a median fovea on upper half; pronotal asperities larger, the tubercles largely absent but replaced by shallow, rather obscure punctures.

Type Locality.—Four km. southwest of Rincon, Osa Peninsula, Puntarenas Prov., Costa Rica.

Host.—*Cecropia* sp.

Type Material.—The male holotype, female allotype, and two paratypes were collected at the type locality between February 21 and 28, 1967, by D. D. Sliwa, from the fallen leaf petiole of a *Cecropia* tree.

The holotype, allotype, and paratypes are in my collection.

Chramesus periosus, n. sp.

Superficially this species resembles *vastus* Wood more closely than other species known to me, although its true affinities may lie nearer to *crenatus* Wood which shared the same host material. From *vastus* it differs by the more closely, deeply punctured pronotum, by the less strongly impressed striae, by the scalelike erect interstitial bristles, and in the male by the frontal impression extending above the eyes.

Male.—Length 2.2 mm. (paratypes 2.0-2.5 mm.), 1.4 times as long as wide, color brown.

Frons broadly concave from epistomal margin to just above upper level of eyes; lateral margins acutely elevated from just below upper level of eyes to epistomal margin, bearing a pointed tubercle at level of antennal insertion; surface reticulate except on smooth epistomal margin, the punctures small, shallow, obscure; vestiture fine, inconspicuous. Antennae as in related species.

Pronotum 0.73 times as long as wide; posterolateral angles one-third pronotum length from base, median area produced posteriorly; sides widest at posterolateral angles, strongly, arcuately convergent to moderate constriction just before the rather broadly rounded anterior margin; surface finely reticulate, with fine, moderately deep, rather close punctures, about half of those in central area finely asperate, the asperities larger toward anterolateral angles; vestiture consisting of stout, rather short, recumbent bristles and similar, very fine hair.

Elytra 0.90 times as long as wide, 1.4 times as long as pronotum; anterior margins armed by low basally fused crenulations that merge lateral to striae 4 into a continuous costa; striae moderately impressed, the punctures small, moderately deep, rather widely spaced; interstriae about twice as wide as striae, weakly convex, a median row of fine, nongranulate punctures and confused minute punctures on each interstriae. Declivity rather steep, convex; sculpture essentially as on disc. Vestiture consisting of ground covering of small, non-overlapping, interstitial scales each longer than wide, and median rows of erect interstitial bristles, each twice as long as ground vestiture and four to five times as long as wide and spaced within a row by slightly more than length of a bristle.

Female.—Similar to male except frons not impressed, almost flat; lateral asperities on pronotum coarsely de-

veloped; each interstriae bearing a uniseriate row of coarse, narrow tubercles, each almost as high as wide.

Type Locality.—Five km. west of Jaltipan, Vera Cruz, Mexico.

Type Material.—The male holotype, female allotype, and 56 paratypes were collected at the type locality on June 25, 1967, 50 m., No. 99, by S. L. Wood, from tunnels in the wood of branches 3-8 cm. in diameter. The host tree, awaiting identification, was also infested by *Chramesus crenatus* and *Scolytus propingus* Blandford.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus maurus, n. sp.

This species resembles *sulcifrons* Chapuis and may be rather closely related; it is easily distinguished, however, by the large tuft of hair on the male scape, by the much coarser asperities on the anterolateral angles of the pronotum, by the coarser sculpture of pronotum and elytra, with some interstriae bearing only one row of interstitial crenulations, and by the median row of coarse setae on each of the interstriae.

Male.—Length 3.0 mm. (paratypes 2.3-3.1 mm.), 1.7 times as long as wide, color very dark brown to black.

Frons similar to but much narrower than in *sulcifrons*; sculpture similar; vestiture above antennal bases much coarser than in *sulcifrons*. Scape bearing a rather large, dense tuft of dark hair.

Pronotum outline as in *sulcifrons*; surface less uniformly, more deeply punctured, some punctures toward base much larger than in *sulcifrons*; anterolateral asperities about twice as large as in *sulcifrons*, the vestiture at lateral margins coarser and longer.

Elytra 1.03 times as long as wide; striae strongly impressed, the punctures clearly indicated; interstriae distinctly less than twice as wide as striae, the punctures subcrenulate on 2 and 3 to declivity, less distinctly so on 4 to 6, the crenulations uniseriate except somewhat biseriate at base of 2; interstriae narrower and more convex toward declivity. Declivity convex, moderately steep; interstriae narrower than on disc, each with a median, subserrate row of low tubercles. Vestiture consisting of a row of short, suberect bristles on each interstriae; each bristle not longer than a third the distance between rows; largely abraded on basal half; some fine hair also on sutural interstriae.

Female.—Similar to male except frons convex, foveate just above level of antennal insertion; tuft of hair on scape absent.

Type Locality.—Near Rincon, Osa Peninsula, Puntarenas Prov., Costa Rica.

Host.—*Ficus* sp.

Type Material.—The male holotype, female allotype, and 30 paratypes were collected at the type locality on August 11, 1966, near 30 m. elevation, No. 63, from a *Ficus* limb 15 cm. in diameter, by S. L. Wood.

The holotype, allotype, and paratypes are

in my collection.

Phloeotribus atavus, n. sp.

The large size, sculpture of the pronotum, and vestiture of pronotum and elytra serve to distinguish this species from all other representatives of the genus.

Female.—Length 3.6 mm. (paratypes 3.3-4.0 mm.), 2.0 times as long as wide; color very dark brown.

Frons shallowly, concavely impressed on lower two-thirds, the impression ending above in a small deep median fovea; lateral margins below antennal bases acute; surface rather coarsely reticulate above fovea, subreticulate to smooth below, the punctures small, deep, close; vestiture inconspicuous. Antennal club with segment 1 three times as wide as long, about as long as scape.

Pronotum 0.96 times as long as wide; widest at or just behind middle, sides rather strongly arcuate, converging very slightly anteriorly, rather strongly constricted just behind the rather broadly rounded anterior margin; surface completely devoid of asperities, reticulate, the punctures rather small, very close, deep; a faint median line weakly elevated; vestiture consisting of inconspicuous, very fine, short hair.

Elytra 1.4 times as long as wide, 1.8 times as long as pronotum; sides straight and parallel on basal two-thirds, broadly rounded and with apex rather narrowly extended on median third behind; striae narrowly impressed, the punctures rather obscure; interstriae twice as wide as striae, crenulate on basal half, some crenulations as wide as interspace, the elevations becoming narrower and uniseriate behind, some fine punctures also present; shining. Declivity rather steep, convex; striae impressed; interstriae convex, 1 slightly elevated on lower half, apical costal margin and posterior part of 9 also slightly elevated, each interspace with a row of small tubercles. Vestiture consisting of moderately sparse, small scales on posterior half of disc and on declivity, and sparse median interstitial rows of fine long hair, longest hairs equal in length to distance between rows and between adjacent hairs within a row.

Male.—Similar to female except frontal impression very slightly deeper and extending to upper level of eyes, the punctures larger, shallower; interspaces 1 and 2 on elytral declivity finely punctured and almost devoid of tubercles.

Type Locality.—Laguna Volcan Poas, Heredia Prov., Costa Rica.

Hosts.—*Clusia* sp. (type), and *Podocarpus oleifolius* (paratype).

Type Material.—The female holotype, male allotype, and 31 paratypes were collected at the type locality on October 6, 1963, at an elevation of about 2,700 m., by S. L. Wood, from a limb of *Clusia* about 25 cm in diameter. Three paratypes bear the same data but were taken July 14, 1963, from a *Podocarpus* root buttress. The egg tunnels were biramous, transverse, and almost entirely in the phloem. The species is aggressive; some specimens were attacking healthy living tissue, and it appeared to have killed several *Clusia* trees in the area.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus hystrix, n. sp.

This species evidently is allied to *discrepans* Blandford, although not closely related. It is distinguished by the more deeply striate elytra, by the more nearly scalelike vestiture, and by the declivital armature.

Male.—Length 1.7 mm. (paratypes 1.7-2.0 mm.), 2.1 times as long as wide; color brown.

Frons very shallowly concave below upper level of eyes, sides weakly elevated and armed at level of antennal insertion by a pair of small tubercles; surface coarsely reticulate, the punctures small, obscure; vestiture sparse, moderately long, coarse. Antennal club with segment 1 three times as wide as long.

Pronotum 0.9 times as long as wide; widest on basal half, the sides weakly arcuate, almost parallel on basal half, then converging to constriction just behind broadly rounded anterior margin; surface coarsely, deeply, closely, irregularly punctured, anterior and lateral areas subgranulate or even very finely asperate; vestiture short, stout, abundant, almost scalelike.

Elytra 1.4 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on basal three-fourths, obtusely angulate behind, with lateral declivital spines interrupting the profile; striae sharply impressed, the punctures large, deep, distinct; interstriae distinctly narrower than striae, irregular, each with a median row of fine setiferous granules and additional subgranulate setiferous punctures on each side. Declivity steep, convex; interspace 1 weakly elevated, 5 with two, 7 with three, 9 with five large pointed tubercles, the posterior most one on each interspace longer, 9 elevated slightly to final spine; costal margin near apex slightly elevated. Vestiture consisting of rather abundant interstitial subsquamose bristles, short except median row twice as long, erect; equally abundant on disc and declivity.

Female.—Similar to male except frons weakly convex, unarmed; pronotum more nearly asperate in lateral areas.

Type Locality.—Rio Damitas in the Dota Mountains, San José Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 20 paratypes were collected at the type locality on February 18, 1964, at an elevation of about 250 m., by S. L. Wood, from the phloem tissues in a stump of a broken unidentified tree 15 cm. in diameter.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus opimus, n. sp.

As in *demessus* Blandford, except smaller, the basal margin of the pronotum straight, and the discal interstriae smooth and shining except for the uniseriate granules.

Male.—Length 1.4 mm. (paratypes 1.4-1.8 mm.), 1.8 times as long as wide; color dark brown, almost black, with light vestiture.

Frons deeply excavated from upper level of eyes to epistoma, deepest near center, the lateral margins acute from middle to antennal bases; surface rather coarsely reticulate; vestiture largely confined to marginal areas. Antennal scape long, ornamented by a tuft of long

yellowish hair. Segment 1 of antennal club three times as wide as long.

Pronotum 0.8 times as long as wide; widest one-third length from base, sides rather strongly arcuate, anterior constriction weak, rather broadly rounded in front; surface coarsely, deeply punctured, spaces between punctures almost smooth, subshining, less than half the width of a puncture, with a small rounded, setiferous granule on anterior margin of each puncture; vestiture consisting of short, stout, whitish bristles.

Elytra 1.1 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on basal two-thirds, broadly rounded behind; single row of crenulations at elytral base high, coarse; striae slightly impressed, the punctures coarse, deep; interstriae convex, narrower than striae, armed by a row of small setiferous tubercles. Declivity steep, convex; striae somewhat narrower and deeper, interspace 9 weakly elevated, more coarsely serrate. Vestiture consisting of uniseriate rows of suberect, flattened bristles, each bristle separated in its own row by distances equal to its own length, and from adjacent rows by distances about equal to one and one-half times its own length.

Female.—Similar to male except frons convex, the lateral margins rounded; and antennal scape without tuft of hair.

Type Locality.—Zamorano, Morazan, Honduras.

Hosts.—*Ficus glabrata* (type), *Ficus* spp. (paratypes), *Celtis iguanae* (paratype), and *Serjania triquetra* (paratype).

Type Material.—The male holotype, female allotype, and 39 paratypes were taken at the type locality on April 18, 1964, at an elevation of 700 m., by S. L. Wood, from the phloem tissues of twigs of *Ficus glabrata*; 35 paratypes bear identical data but were taken from *Serjania triquetra*; 1 bears the same data but is from *Celtis iguanae*; 16 paratypes were collected at the lower Rio Tempisque, Guanacaste Prov., Costa Rica, on March 25, 1964, at 15 m. elevation from *Ficus* twigs; 1 paratype is from Rio Damitas in the Dota Mountains, San José Prov., Costa Rica, taken on February 18, 1964, 200 m. elevation, from an unknown branch; and 1 paratype is from Palin, Esquinla Prov., Guatemala, taken on May 19, 1964, at 300 m. elevation, from a *Ficus* twig; all were collected by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus squamatus, n. sp.

This unique species is distinguished from other species in the genus by the small size, by the unarmed pronotum, by the short, squamose vestiture, by the shallowly impressed male frons, and by other characters.

Male.—Length 1.25 mm. (allotype 1.3 mm.), 2.1 times as long as wide; color black, with white squamose vestiture.

Frons shallowly concave from upper level of eyes to epistoma, the lateral margins not acutely elevated

or armed; epistomal margin weakly elevated, and with a median tubercle; surface coarsely reticulate; vestiture inconspicuous, mostly confined to marginal areas. Antennal club small, compact; segment 1 about 1.5 times as wide as long.

Pronotum 0.8 times as long as wide; widest just behind middle, sides moderately arcuate, moderately constricted just behind the rather narrowly rounded anterior margin; surface rather coarsely reticulate including the punctures, with close, coarse, shallow punctures; vestiture consisting of suberect, short, stout, almost scalelike bristles, most of them about three times as long as wide.

Elytra 1.4 times as long as wide, 1.9 times as long as pronotum; crenulations of elytral base coarse, rather high, forming a single row; striae weakly impressed, the punctures large, rather deep; interstriae about half as wide as striae, almost restricted to a narrow row of closely set, subvulcanate, squamiferous punctures. Declivity rather steep, convex; striae somewhat narrower and deeper than on disc. Vestiture consisting of uniseriate rows of erect interstitial scales, each scale less than twice as long as wide; separated from adjacent scales in the same row by distances equal to less than the width of a scale, and between rows by distances equal to almost twice the length of a scale.

Female.—Similar to male except frons convex, the median epistomal tubercle absent; vestiture of pronotum and elytra very slightly more slender.

Type Locality.—Tapanti, Cartago Prov., Costa Rica.

Type Material.—The male holotype and female allotype were collected at the type locality on July 8, 1963, at an elevation of 1,300 m., by S. L. Wood, from a dying tree that bore fruiting pods.

The holotype and allotype are in my collection.

Chaetophloeus phorodendri, n. sp.

This species has the same arrangement of crenulations at the base of the elytra as *braziliensis* (Blackman), but it differs by the much larger size, by the reduction of elytral striae, by the very different vestiture and by other characters.

Male.—Length 1.8 mm. (paratypes 1.5-2.0 mm.), 1.4 times as long as wide; color black, vestiture cinereous.

Frons broadly, deeply concave from vertex to the broadly emarginate epistomal margin, and from eye to eye; surface granulose-reticulate; vestiture sparse in concavity, a few erect gray setae along sides below eye, margin above eyes ornamented by a row of long reddish hair many of which reach mandibles; mandibles each with an anterior extension half as large as mandible. Antennal club about as in *braziliensis*.

Pronotum 0.53 times as long as wide; widest at base, strongly arcuately converging to the broadly rounded anterior margin; surface reticulate, with small, rather close setiferous punctures; lateral areas armed by two groups of asperities; vestiture consisting of mixed slender and stout, short bristles and a few bifid hairs in lateral areas.

Elytra 1.1 times as long as wide, 2.1 times as long as pronotum; anterior margins armed by six pairs of crenulations, the median pair twice as wide as others, an additional submarginal pair at base of interspace 1;

striae reduced, obscure, the punctures only slightly larger than those of interspaces; interspaces wide, flattened, with numerous punctures variable in size. Declivity steep, convex. Vestiture consisting of short, rather abundant, slender scales, and median rows of erect interstitial scales, each scale about three times as long as wide, separated from other scales in same row by distances equal to length of scale and between rows by one and one-half times length of a scale.

Female.—Similar to male except frons flattened, with a small median impression, frontal vestiture short, not specialized; pronotum armed by three paired groups of asperities.

Type Locality.—Zamorano, Morazan, Honduras.

Host.—*Phoradendron robustissimum* (type), and *Phoradendron* sp. (paratypes).

Type Material.—The male holotype, female allotype, and 40 paratypes were collected at the type locality on April 18, 1964, at an elevation of 700 m., by S. L. Wood, from twigs of the above mistletoe; 4 paratypes were taken at Cañas, Guanacaste Prov., Costa Rica, on April 10, 1966, from *Phoradendron* twigs; one paratype was taken 20 km. southeast of Liberia, Guanacaste Prov., Costa Rica, on July 10, 1966, from *Phoradendron* twigs; all were collected by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Liparthrum americanum, n. sp.

This species is allied to *squamosum* (Blackman), but is readily distinguished by the much smaller, more strongly impressed elytral striae, and by the broadly concave male frons.

Male.—Length 0.8 mm., about 2.1 times as long as wide; color rather light brown.

Frons shallowly concave almost from eye to eye and from vertex to epistoma; surface reticulate; vestiture largely confined to impressed area, consisting of very fine, minute, abundant, pilose hair of uniform length.

Pronotum 0.8 times as long as wide; widest one-third from base, sides moderately arcuate, rather narrowly rounded in front; surface obscured by vestiture, evidently minutely subgranulate and with small setiferous granules uniformly distributed; vestiture consisting of stout recumbent bristles and erect broad scales in about equal numbers.

Elytra 1.3 times as long as wide, 1.7 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind; bases armed by six pairs of crenulations between striae 4; striae not impressed, the punctures rather large, deep; interstriae almost as wide as striae, weakly convex, the moderately large, setiferous punctures uniseriate, feeble granulate on anterior side. Declivity steep convex; striae and interstriae somewhat narrower than on disc. Vestiture consisting of stria rows of short recumbent, stout hair, and interstitial rows of erect, broad scales, each scale almost as wide as long.

Type Locality.—The lower Rio Tempisque, Guanacaste Prov., Costa Rica.

Host.—*Ficus* sp.

Type Material.—The unique male holotype was collected at the type locality on March 25, 1964, at an elevation of about 20 m., by S. L. Wood, from small branches of the common narrow leaved fig that grew near the river.

The holotype is in my collection.

A second specimen, tentatively assigned to this species, possible the female, is identical to the type except the frons is less deeply, less extensively impressed and the pilose vestiture is not evident. It was taken at Dominical, Puntarenas Prov., Costa Rica, on December 9, 1963, from an unidentified branch.

Liparthrum cracentis, n. sp.

This species is allied to the four previously described American species but it may be distinguished by the small size, by the more slender body form, by the poorly developed female frontal vestiture, and by the narrower elytral scales.

Female.—Length 0.8 mm. (paratypes 0.75-0.85 mm.), 2.2 times as long as wide; color brown.

Frons moderately convex, slightly impressed just above epistomal margin; surface rather coarsely reticulate; vestiture sparse, more conspicuous toward epistoma, consisting of stout, subplumose setae. Eye and antenna as in allied species.

Pronotum 0.81 times as long as wide; widest on basal third, sides weakly arcuate from base, converging on anterior half to the broadly rounded anterior margin; surface shining, feebly subreticulate, the obscure, setiferous punctures rather close, their anterior margins very finely asperate. Vestiture consisting of truncate, subtriangular scales, each about one and one-half times as long as wide, and equally abundant stout hairlike setae, each about one and one-half times as long as scales.

Elytra 1.6 times as long as wide, 1.96 times as long as pronotum; basal margins armed by five pairs of crenulations between interstriae 4; striae not impressed, the punctures coarse, rather deep; interstriae about half as wide as striae, the punctures fine, uniseriate, evidently not granulate. Declivity rather steep, convex; sculpture about as on disc. Vestiture consisting of striae rows of bristles equal in length to scales in interstitial rows; each scale almost as wide as a striae puncture and slightly longer than wide.

Male.—Similar to female except pronotum bearing a pair of small, median tubercles on anterior margin and a smaller submarginal pair about one-fourth pronotum length from anterior margin.

Type Locality.—Twenty-nine km. west Niltipee, Oaxaca, Mexico.

Type Material.—The female holotype, male allotype, and 29 paratypes were collected at the type locality on June 23, 1967, at about 30 m. elevation, by S. L. Wood, from the phloem of small twigs of a small tree having narrow, thick, waxy, simple leaves. The identification of the host is not yet available.

The holotype, allotype, and paratypes are in my collection.

Cnemonyx nitens, n. sp.

Evidently allied to *atratus* (Blandford), but distinguished by the more extensive frontal impression of the male, by the elongate pronotal punctures and minutely, longitudinally strigose pronotal surface, and by the coarser interstitial punctures of the elytra.

Male.—Length 2.5 mm. (paratypes 2.0-2.5 mm.), 2.1 times as long as wide; color almost black.

Frons shallowly concave on median half from upper level of eyes to epistoma; surface reticulate above, the punctures rather coarse, deep, close, becoming finer and closer below in concave area; vestiture short and rather abundant in concave area, longer at sides of this area, evidently glabrous elsewhere. Antennal club subtriangular, finely, closely covered by hairlike pubescence; sutures not evident.

Pronotum 1.0 times as long as wide; widest at base, sides weakly arcuate and converging slightly to the slight constriction just behind the broadly rounded anterior margin; surface shining, shallowly etched by minute, longitudinally strigose lines, becoming reticulate anteriorly, the punctures fine and elongate posteriorly, almost round and larger anteriorly and laterally; glabrous.

Elytra 1.2 times as long as wide, 1.3 times as long as pronotum; sides straight and parallel on basal half, then arcuately converging to the rather narrowly rounded, suturally subemarginate, posterior margin; striae 1 weakly, others feebly impressed, the punctures rather small, deep, close; interstriae smooth, shining, about twice as wide as striae, the punctures about half as large as those of striae, uniseriate behind, moderately confused on anterior half of disc; elytral bases with fine raised line; base of interspace 1 not depressed; scutellum small, as wide as long, almost flush with elytral surface. Declivity moderately steep, convex; striae and interstriae narrower than on disc, the striae narrowly impressed; interstriae moderately, broadly convex, shining except sutural half of 1 dull, the punctures uniseriate. Vestiture confined to declivity, consisting of sparse minute, short, suberect scales arising from interstitial punctures.

Female.—Similar to male except frons flattened, the vestiture reduced; strigose lines on pronotum rather obscure; interstitial punctures on elytral disc not as confused; and surface of declivity less brightly shining.

Type Locality.—Puerto Viejo, Heredia Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 34 paratypes were collected at the type locality on March 12, 1964, at an elevation of about 70 m., by S. L. Wood, from bark of the limb of a fallen tree.

The holotype, allotype, and paratypes are in my collection.

Cnemonyx insignis, n. sp.

This species evidently is allied to *panamensis* (Blandford), but is distinguished by the larger size, by the procurved epistomal carina, and by other characters.

Male.—Length 3.5 mm. (paratypes 3.5-3.9 mm.), 2.0 times as long as wide; color dark brown.

Frons shallowly concave on median two-thirds from upper level of eyes to epistoma; surface reticulate-gran-

late, and closely, deeply, rather coarsely punctured in concave area, shallowly, less closely punctured above; slightly less than median half of epistoma armed by an elevated, procurved, transverse carina; vestiture confined to concavity, consisting of short, erect, rather abundant, dark hair.

Pronotum 0.9 times as long as wide; widest at base, the sides weakly arcuate and converging toward the rather broadly rounded anterior margin; surface smooth and shining on posterior three-fourths, with minute points and fine punctures, anterior fourth rather coarsely subreticulate, dull, faintly, longitudinally etched in lateral areas, the punctures very slightly larger in anterior area, much larger laterally; glabrous.

Elytra 1.1 times as long as wide, 1.2 times as long as pronotum; scutellum as wide as long, not depressed; basal margins of elytra with an irregular raised line; outline as for *nitens*, above; striae rather strongly impressed, the punctures fine, shallow, distinct; interstriae smooth, shining, at least twice as wide as striae, moderately convex at base, becoming rather narrowly costiform by declivital base, the punctures fine and uniseriate behind, confused toward base. Declivity moderately steep, convex; striae broadly impressed, the fine shallow punctures evident; interstriae narrowly, acutely, subserrately elevated; striae and interstriae minutely reticulate-granulate; costal margin rather coarsely serrate. Rows of very minute interstitial scales evident on declivity.

Female.—Presumably the female is represented by specimens having the frons less strongly impressed, but otherwise similar to the male.

Type Locality.—Moravia, Cartago Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 5 paratypes were taken at the type locality on March 11, 1964, at an elevation of about 500 m., by S. L. Wood, as dead specimens under loose bark of an unidentified log about 40 cm. in diameter.

The holotype, allotype and paratypes are in my collection.

Cnemonyx opacus, n. sp.

This species, at least superficially, resembles *insignis* Wood, above, but is easily distinguished by the smaller size, by the narrow frontal carina, by the much more extensively granulate elytra, and by characters mentioned in the key. However, the antennal club has an entirely different shape and has three strongly procurved sutures clearly marked by rows of setae suggesting that the relationship is superficial at best.

Male.—Length 2.2 mm. (paratypes 2.0-2.5 mm.), 2.2 times as long as wide; color dark brown.

Frons shallowly concave on median half from upper level of eyes almost to epistoma, the surface closely, deeply, rather coarsely punctured; median fourth of epistoma bearing a strongly elevated, procurved, transverse carina; vestiture consisting of short, erect, rather abundant, stout hair in concave area. Antennal funicle with inner angle of segments projecting and bearing tufts of long yellow hair; club obovate, longer than wide, with three strongly procurved sutures conspicuously marked by rows of closely set setae.

Pronotum about as wide as long; widest on basal third, the sides rather weakly arcuate and converging to the weak, transverse constriction just behind the rather narrowly rounded anterior margin; surface smooth and shining behind, becoming reticulate anteriorly and toward lateral margins, the punctures rather coarse, deep, close, somewhat larger in lateral areas; glabrous.

Elytra 1.2 times as long as wide, 1.3 times as long as pronotum; sides straight and parallel on more than basal half, rather narrowly rounded behind; scutellum very small, rounded, not depressed; basal margins of elytra marked by a fine, irregular, raised line; striae impressed, the punctures rather large, deep, clearly impressed in basal area, obscure behind; interstriae convex, finely, completely granulate (including striae) posteriorly, coarsely punctured on basal third of disc. Declivity moderately steep, convex, striae deeply impressed, the punctures obscure; interstriae narrow, strongly convex, minutely granulate, finely subserrate; interspace 9 moderately elevated, continuing to apex, highest at junction with 3. Vestiture confined to declivity, consisting of uniseriate rows of minute interstitial scales.

Female.—Similar to male except frons less strongly impressed, almost flat.

Type Locality.—Playa del Coco, Guanacaste, Costa Rica.

Host.—*Hippomane mancinella*.

Type material.—The male holotype, female allotype, and 64 paratypes were collected at the type locality on October 18, 1963, at sea level, by S. L. Wood, from the bark of the above host tree. This aggressive species constructs biramous, transverse, egg tunnels in the bole and branches of the host tree. Adult and the irregular larval tunnels were almost entirely in the phloem tissues.

The holotype, allotype, and paratypes are in my collection.

Cnemonyx gracilens, n. sp.

This species is very closely related to *exilis* Wood, but it may be distinguished by the smaller size, by the more broadly impressed frons with the epistomal carina higher, by the less numerous, more nearly oval pronotal punctures, and by the shorter, finer, less strongly flattened elytral setae.

Male.—Length 1.3 mm. (paratypes 1.2-1.4 mm.), 2.6 times as long as wide; color dark brown.

Frons as in *exilis* but more broadly planoconcave, the transverse epistomal carina less procurved, slightly higher, occupying at least two-thirds width of epistomal margin; pubescence perhaps a little more abundant.

Pronotum 1.09 times as long as wide; punctures distinctly less numerous than in *exilis*, each about one and one-half times as long as wide. Glabrous.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; as in *exilis* interstitial bristles on declivity much shorter, very weakly or at all flattened, narrower, not increasing in width apically.

Female.—Similar to male except frons less strongly impressed.

Type Locality.—Fifty-seven km. southeast of

El Cameron, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 98 paratypes were collected at the type locality on June 22, 1967, No. 81, by S. L. Wood. Specimens were taken from phloem tissues of twigs of a small tree that had peeling bark, thin simple leaves, and abundant white latex; a sample awaits identification.

The holotype, allotype and paratypes are in my collection.

Cnemonymx recavus, n. sp.

This species is allied to *impressus* Wood, but it is readily distinguished by the larger size, by the much more strongly impressed frons and by the dull pronotal surface.

Male.—Length 1.7 mm. (paratypes 1.5-1.8 mm.), 2.1 times as long as wide; color dark reddish brown.

Frons broadly, rather deeply concave from just below upper level of eyes to epistomal margin; concavity densely pubescent, the setae moderately, uniformly long; surface of marginal areas and above coarsely reticulate, with fine, close punctures; surface in concavity obscured by pubescence. Scape short; funicle bearing a dense tuft of long hair; club obovate, with three strongly procurved sutures marked by setae, 1 extending almost two-thirds club length from base.

Pronotum 0.92 times as long as wide; basal margin bisinuate, marked by a fine, raised line; widest at base, arcuately converging to a slight constriction just before the broadly rounded anterior margin; surface dull, minutely, longitudinally etched, the punctures fine, oval, close, moderately deep. Glabrous.

Elytra 1.2 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on slightly more than basal half, rather narrowly rounded behind; basal margins indistinctly raised along a fine line; striae impressed, the punctures fine, distinctly impressed; interstriae almost twice as wide as striae, convex, dull, each with a uniseriate (confused on 2) row of fine, short, transverse crenulations, the puncture posterior to each crenulation fine, obscure. Declivity convex, moderately steep; about as on declivity, with interstriae 9 weakly elevated and more coarsely tuberculate, 10 with a row of fine tubercles posteriorly. Vestiture confined to declivity, consisting of interstitial rows of very short, flattened bristles each about twice as long as wide.

Female.—Similar to male except frons very slightly less strongly impressed.

Type Locality.—Forty-eight km. east of Tehuantepec, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 87 paratypes were collected at the type locality on June 22, 1967, 120 m., No. 84, by S. L. Wood. The host was a small tree with simple leaves; a sample awaits identification.

The holotype, allotype, and paratypes are in my collection.

A series taken from "Leche Sillo," 16 km. northwest of Acatlan, Puebla, Mexico, June 15, 1967, 1,700 m., No. 36, by S. L. Wood, not designated as paratypes, have the posterior half of the pronotum smooth and shining, and the punctures

behind the interstitial crenulations are more conspicuous. The series overlap in these characters to such an extent that geographical races cannot be designated.

Camptocerus infidelis, n. sp.

This species is allied to *auricomus* Blandford, but is not closely related. It differs in the female by the more strongly convex frons above, and narrower below, by the much less closely punctured pronotum, by the more sparsely punctured elytra, by the near absence of elytral scales, by the smaller size, and by other characters.

Female.—Length 2.7 mm. (paratypes 3.2 mm.), 2.0 times as long as wide; color black.

Frons rather strongly convex above, more nearly flattened below, with a distinct, transverse impression just above epistomal margin; surface rather coarsely reticulate and with rather abundant, shallow, indefinite punctures; vestiture sparse, inconspicuous. Antenna essentially as in *auricomus*.

Pronotum 0.98 times as long as wide; widest near base, sides rather weakly arcuate and converging slightly to the rather strongly rounded anterior angles, broadly rounded in front; surface minutely reticulate and dull on anterior half, almost smooth and subsining behind; the punctures minute, sharply impressed, separated by distances equal to two or more diameters of a puncture; glabrous.

Elytra 1.2 times as long as wide, 1.3 times as long as pronotum; widest at base, the sides converging posteriorly to the narrow, subemarginate posterior margin; striae not impressed, the punctures small, shallow, rather widely spaced; interstriae twice as wide as striae, shining, somewhat irregular, very sparsely punctured, the shallow punctures almost as large as those of striae. Declivity gradual, convex; striae weakly impressed. Vestiture consisting of very sparse interstitial scales on sides and declivity.

Male.—Not represented in the material at hand.

Type Locality.—Peralta, Cartago Prov., Costa Rica.

Type Material.—The female holotype and one female paratype were collected at the type locality on March 10, 1964, at an elevation of about 500 m., by S. L. Wood, from a dead tree seedling 1 cm. in diameter. The egg tunnel followed the central axis of the host for several centimeters, the larval cradles extended into the wood at an acute angle to the central axis. Two adult females and small larvae were in the only tunnel found.

Both specimens are in my collection.

Scolytus nodatus, n. sp.

Fig. 1

In the American *Scolytus* fauna this species is unique. The female abdominal sterna are unarmed; in the male sternum 2 is armed by a large median tooth, 4 is armed by a large, median, rounded knob, and the lateral margins of 2 and 3 are each armed by a pair of small teeth; the frons is convergently aciculate and pubescent in

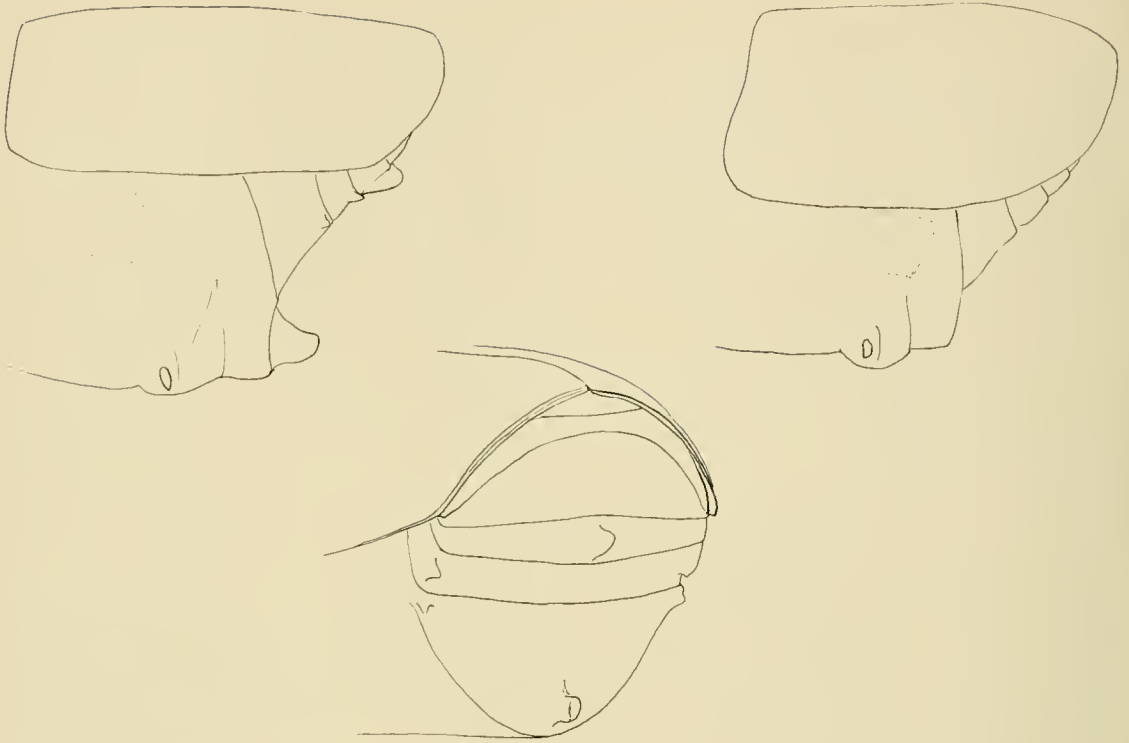


Fig. 1. *Scolytus nodatus* abdomen and elytra: male at upper left and below; female at upper right.

both sexes, it is devoid of tubercles in both sexes.

Male.—Length 3.8 mm. (paratypes 3.1-3.8 mm.), 2.0 times as long as wide; color dark brown, anterior margin of thorax, bases and apices of elytra may be reddish.

Frons weakly convex; surface coarsely, somewhat convergently strigose toward the shallowly, broadly emarginate epistomal margin; punctures not evident; vestiture consisting of fine, rather long, moderately abundant hair. Eye emarginate; very finely granulate. Antennal club 2.0 times as long as wide; sutures not evident, very finely, closely pubescent.

Pronotum equal in length and width; widest at base, the sides moderately arcuate and converging to distinct constriction just behind broadly rounded anterior margin; surface smooth, brightly shining, the punctures rather small, deep, oval, larger in lateral and anterior areas; glabrous on disc, sparse hair at sides and in front.

Elytra 1.1 times as long as wide, 1.1 times as long as pronotum; sides straight and parallel on basal half, converging slightly behind to the broadly rounded posterolateral angles, almost straight on median half; posterior margin smooth, striae and interstriae moderately impressed, the punctures small, rather deep, those of striae very slightly larger; elytra descending very slightly near posterior margin; vestiture confined to scutellar impression. Sternum 2 ascending sharply, the margin not produced, armed by a laterally compressed, median spine, its base extending from anterior margin to middle of segment, longitudinal length of base and height of spine about equal; sternum 4 armed by a large, rounded tubercle, 2 and 3 each armed at lateral margins by a pair of small teeth; surface finely, obscurely punctured, dull except anterior half of 2 shining; pubescence sparse, hairlike.

Female.—Similar to male except frons more nearly flat; all abdominal sterna unarmed.

Type Locality.—Santa Ana, San José Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 4 paratypes were taken at the type locality on November 8, 1963, at an elevation of 1,300 m., by S. L. Wood, from the limb of an unidentified tree. Nineteen other paratypes were collected at Fort Clayton, Panama Canal Zone, on December 22, 1963, at an elevation of 30 m., by S. L. Wood, from a large, woody vine (liana) about 5 cm. in diameter.

The holotype, allotype, and paratypes are in my collection.

Scolytus cristatus, n. sp.

Fig. 2

This species does not appear to be closely related to any known Neotropical representative of the genus. The frons of both sexes is convex, convergently strigose, with a very fine, low, long, median, subcarinate ridge, and in the male moderately abundant, uniformly distributed, long, frontal hair; the second abdominal sternum ascends rather abruptly, not sharply, and is armed by a high, narrow carina on anterior two-thirds, its highest point near its posterior extremity.



Fig. 2.

Scolytus cristatus posterolateral aspect of male abdomen.

Male.—Length 2.4 mm. (paratypes 2.3–2.7 mm.). 2.0 times as long as wide; color reddish-brown (mature paratypes dark reddish-brown).

Frons convex, somewhat flattened below; surface convergently strigose, the grooves usually wider than the ridges, the median ridge higher, subcarinate, extending from epistomal margin almost to upper level of eyes; vestiture fine, long, rather abundant, uniformly distributed.

Pronotum very slightly wider than long; widest on basal third, sides moderately arcuate and converging slightly to constriction just behind the broadly rounded anterior margin; surface smooth, shining, with some very minute points and rather widely separated, moderately small, deep, oval punctures, the punctures larger in lateral areas and in front; glabrous.

Elytra 1.1 times as long as wide, 1.2 times as long as pronotum; striae and interstriae strongly, equally impressed, the punctures moderately large, shallow, the ridges between rows of punctures smooth, shining, convex, almost as wide as grooves; declivity descending slightly; a few scattered, slender scales on declivity. Venter with sternum 2 ascending abruptly, not sharply, armed by a median, laterally compressed, rather high elevation extending from near anterior margin of segment two-thirds of its length, highest point on elevation near its posterior limits; sternum 2 very coarsely, shallowly punctured, the surface within each puncture reticulate, the interspaces subreticulate; sternum 3 with one row of punctures, 4 and 5 not clearly punctured, dull.

Female.—Similar to male except frons subglabrous; carinate armature of sternum 2 not as high, occupying middle third of length of segment.

Type Locality.—Lower Rio Tempisque, Guanacaste Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 29 paratypes were collected at the type locality on March 25, 1964, at an elevation of about 20 m., by S. L. Wood, from the bark of an unidentified broken branch. The transverse, biramous egg tunnels engraved the wood rather deeply; larvae were not present.

A series of this species, not included in the type series, was collected 8 km. south of Atenquique, Jalisco, Mexico, on June 25, 1965, from an unidentified woody vine (liana).

The holotype, allotype, and paratypes are in my collection.

Microborus limatus, n. sp.

This species differs from all previously described representatives of this genus by the more

narrowly rounded (subangulate) posterior margin of the elytra, by the more gradual elytral declivity, and, particularly, by the brightly shining subglabrous elytral surface with the sparse, declivital, hairlike setae that are separated from one another by one to two or more times the length of a seta.

Male.—Length 1.4 mm. (paratypes 1.3–1.5 mm.), 2.7 times as long as wide; body color dark brown, elytra medium brown.

Frons narrow and feebly convex between eyes, protruding very slightly just above antennal bases; surface smooth and polished, with a few scattered, minute punctures; almost glabrous. Eyes very large, almost touching below; anterior margin very broadly emarginate; very coarsely faceted. Antennal scape short, about twice as long as pedicel; funicle 6-segmented; club subglobular, sutures obscurely marked by rows of setae.

Pronotum 1.25 times as long as wide; sides almost straight and parallel on basal three-fourths, rather broadly rounded in front; anterior angles not narrowed; surface shining, weakly reticulate, the punctures rather small and shallow, separated from one another by one to two diameters; glabrous.

Elytra 1.9 times as long as wide; sides almost straight and parallel on basal three-fourths, narrowly (subangulate) rounded behind; striae 1 moderately, 2 weakly impressed, narrow, the punctures small, separated by distances equal to their own diameters; interstriae distinctly wider than striae, smooth, brightly shining, each with a sparse row of minute punctures. Declivity rather steep, not precipitous; striae and interstriae about as on disc, except interstitial punctures very finely granulate; interspaces 7 and 9 acutely elevated from declivital base to point of fusion, the acute elevation continuing to apex. Vestiture short, sparse, almost entirely restricted to declivity; each hairlike seta about equal to half the width of an interspace, and separated from one another by about one and one-half to two times the length of a setae.

Female.—Similar to male except more finely sculptured; the declivital granules scarcely visible.

Type Locality.—Finca Gromaco on Rio Coto Brus (34 km. from mouth), Puntarenas Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 11 paratypes were taken at the type locality on July 14, 1963, at an elevation of about 500 m., by S. L. Wood, from the phloem tissues of a large limb of an unknown tree that had been cut at the margin of the jungle.

The holotype, allotype, and paratypes are in my collection.

Microborus ambitus, n. sp.

This species is closely related to *limatus* Wood, described above, but it may be distinguished by the slightly deeper pronotal punctures, by the impressed, much more coarsely punctured declivital striae, and by the fine interstitial granules on the declivity.

Female.—Length 1.3 mm. (paratypes 1.3–1.4 mm.), 2.9 times as long as wide; color of head and pronotum very dark brown, posterior areas and legs reddish brown.

Head, pronotum, and elytral disc as in *limatus* except, as noted above, the pronotal punctures slightly deeper. Elytral declivity convex, steep; striae slightly impressed, the punctures coarse, deep; interstriae slightly narrower than striae, very slightly convex, each bearing a uniseriate row of fine granules; interstriae 7 very acutely, strongly elevated, joining 9 and continuing but declining in height slightly along costal margin to sutural apex, 9 narrowly, not strongly elevated from level of hind coxae to junction with 7. Vestiture confined to declivity, consisting of interstitial rows of fine, short, almost hairlike bristles.

Male.—Although both sexes are probably represented in the series sexual differences are not apparent.

Type Locality.—Twenty-five km. east of Coatzacoalcas, Veracruz, Mexico.

Type Material.—The female holotype and two paratypes were collected at the type locality on June 26, 1967, 30 m., No. 110, by S. L. Wood. Three paratypes were taken 22 km. west of Cardenas, Tabasco, Mexico on June 26, 1967, 30 m., No. 106, by S. L. Wood. Both series were taken from phloem tissues of limbs and bole 10-20 cm. in diameter of the same unidentifiable species of cut tree.

The holotype and paratypes are in my collection.

Scolytodes (s. str.) clusiae, n. sp.

Evidently not closely related to previously known species. It has interstriae 10 ending before level of metacoxae, the protibiae armed by a small tooth on posterior face just before tarsal insertion and between terminal mucro and first or second marginal tooth; female frons broadly, shallowly concave.

Female.—Length 1.8 mm. (paratypes 1.7-1.9 mm.), 2.4 times as long as wide; color black.

Frons broadly, shallowly concave from upper level of eyes to level of antennal insertion; surface closely, deeply, somewhat coarsely punctured over entire frontal area in and out of concavity; median epistomal lobe conspicuous, broad, short, continuous with surface of frons; vestiture very fine, not abundant, longer above, not evident along epistoma.

Pronotum 1.0 times as long as wide; widest at base, very slightly constricted one-third from base, weakly arcuate on anterior half then broadly rounded in front; surface reticulate, with fine, obscure, rather widely spaced punctures on posterior half, equally fine sparse, minute granules on anterior third; almost glabrous.

Elytra 1.4 times as long as wide, 1.7 times as long as pronotum; widest one-third from base, the sides feebly arcuate, abruptly rounded at declivital base, narrowly rounded behind; striae not impressed, the punctures very small, not deep; interstriae about twice as wide as striae, shining, irregular due to obscure surface lines, the punctures not evident. Declivity convex, rather steep; striae 1 weakly impressed above, the punctures on all striae obscurely indicated. Vestiture consisting of a few rather short hairs and, on lower half, more numerous, very short, semirecumbent hair.

Male.—Similar to female except frons rather strongly convex, finely, obscurely punctured, surface reticulate, vestiture sparse, short, inconspicuous; striae punctures rather obscure.

Type Locality.—Summit of Volcan Poas, Heredia Prov., Costa Rica.

Host.—*Clusia* sp.

Type Material.—The female holotype, male allotype, and 16 paratypes were collected at the type locality on August 19, 1966, by S. L. Wood, from green phloem of dying twigs of the common *Clusia* tree in the area.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (s. str.) volcanus, n. sp.

Closely related to *clusiae* Wood, described above, but smaller, the small tooth on posterior face of protibiae absent, the striae punctures larger, and the female frons more narrowly impressed to vertex.

Female.—Length 1.3 mm. (paratypes 1.2-1.4 mm.), 2.3 times as long as wide; color very dark brown, almost black.

Frons narrowly, shallowly concave from epistomal margin to above upper level of eyes; surface finely, shallowly but distinctly, densely punctate, epistomal lobe mostly shining; vestiture largely confined to margin of impressed area, fine, short below, somewhat longer above, moderately abundant, minute in concavity.

Pronotum 1.1 times as long as wide; sides almost straight and parallel on basal half, then somewhat arcuate and rather narrowly rounded in front; surface reticulate, the punctures fine, sparse, rather obscure, devoid of granules; glabrous.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, narrowly rounded behind; striae not impressed, the punctures moderately large, deep; interstriae slightly wider than striae, shining, with very few lines, the punctures obscure, mostly obliterated. Declivity rather steep, convex; an occasional deep, interstitial puncture present; shining. Glabrous.

Male.—Similar to female except frons convex, reticulate, obscurely punctured, the vestiture greatly reduced, inconspicuous; a few interstitial punctures clearly impressed.

Type Locality.—Volcan Poas, Heredia Prov., Costa Rica.

Type Material.—The female holotype, male allotype, and 24 paratypes were collected at the type locality on July 14, 1963, 100 m. (elevation) below the summit, by S. L. Wood, from a small woody vine and cut tree seedlings.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (s. str.) parvulus, n. sp.

Similar to *vulcanus* Wood, described above, but smaller, the female frons armed by a pair of longitudinal carinae, the striae punctures reduced; the female frontal vestiture uniformly distributed.

Female.—Length 1.1 mm. (paratypes 0.9-1.1 mm.), 2.3 times as long as wide; color rather dark brown.

Frons flattened from upper level of eyes to epistoma, the median half of each side just inside of lateral margin armed by a shining longitudinal carina; the pair of carinae beginning at level of antennal insertion and ending before upper level of eyes; surface finely, rather closely punctured in impressed and lateral areas, reticulate above eyes; vestiture fine, moderately long around margin, somewhat shorter in central area, moderately abundant.

Pronotum 1.0 times as long as wide; sides very weakly arcuate and feebly narrowed anteriorly on basal two-thirds, broadly rounded in front; surface reticulate, with sparse, minute punctures extending from base to anterior margin; glabrous.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal half, rather narrowly rounded behind; striae 1 weakly impressed, others not at all impressed, the punctures fine, shallow, rather obscure; interstriae wider than striae, not entirely smooth, the punctures sparse, fine, obscure. Declivity convex, steep; essentially as on disc but interspaces narrower and punctures smaller, the features not sharply defined. Vestiture consisting of less than a dozen moderately long, erect interstitial bristles.

Male.—Similar to female except frons convex, with a slight transverse impression just above epistoma, surface obscurely reticulate, shining, sparsely punctured, vestiture very sparse, mostly near epistoma; pronotum obscurely reticulate, subshining.

Type Locality.—Pandora, Limón Prov., Costa Rica.

Host.—*Cecropia* sp.

Type Material.—The female holotype, male allotype, and 12 paratypes were collected at the type locality on August 23, 1963, at an elevation of about 50 m., by S. L. Wood, from *Cecropia* leaf petioles.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (s. str.) acares, n. sp.

Allied to *parvulus* Wood, described above, but the female frontal vestiture longer and much more abundant near vertex, and the pronotal punctures more coarsely, deeply impressed in posterior area.

Female.—Length 1.1 mm. (paratypes 0.9-1.1 mm.), 2.4 times as long as wide; color dark brown.

Frons narrowly flattened from well above upper level of eyes to epistoma, margined at sides by a pair of shining, longitudinal carinae extending almost from epistoma (half way between level of antennal insertion and epistomal margin) to near upper level of eyes; surface sculpture obscure between carinae, evidently smooth and finely punctured; vestiture largely confined to vertex above upper level of eyes, consisting of a dense, long brush of subplumose, yellow hair that extends in length to a point below level of antennal bases.

Pronotum and elytra as in *parvulus* (above), except pronotum more narrowly rounded in front and its punctures somewhat larger.

Male.—Similar to female except frons convex with a slight transverse impression just above epistoma, the surface reticulate, sparsely punctured, the vestiture reduced to a few setae near epistoma.

Type Locality.—Rio Damitas in the Dota Mountains, San José Prov., Costa Rica.

Host.—*Cecropia* sp.

Type Material.—The female holotype, male allotype, and 14 paratypes were collected at the type locality on August 22, 1963, at an elevation of about 250 m., by S. L. Wood, from the petioles of fallen *Cecropia* leaves. Other paratypes were taken from the same host material, by S. L. Wood, as follows: 17 from Barro Colorado Island, Panama Canal Zone, December 27, 1963, elevation about 70 m.; 11 from Palin, Esquintla Prov., Guatemala, May 19, 1964, elevation 350 m.; 1 from Rincon de Osa, Puntarenas Prov., Costa Rica, August 11, 1966, elevation 30 m.

The holotype, allotype, and paratypes are in my collection.

Scolytodes irazuensis, n. sp.

Rather closely related to *parvulus* Wood, described above, but larger, the female frons only shallowly impressed with setae on vertex extending half the distance to the antennal insertion, and the general sculpture coarser.

Female.—Length 1.7 mm. (paratypes 1.5-1.9 mm.), 2.4 times as long as wide; color very dark brown.

Frons rather broadly, longitudinally impressed from upper level of eyes to epistoma; the lateral margins above level of antennal insertion subcarinately elevated almost to upper level of eyes; surface finely, closely, deeply punctured; vestiture mostly confined to vertex, rather long, moderately abundant (largely abraded in type), none of setae long enough to reach half the distance to level of antennal insertion, only a few setae arise below upper level of eyes.

Pronotum 1.0 times as long as wide; sides weakly arcuate and converging slightly on basal two-thirds, rather broadly rounded in front; surface reticulate, rather coarsely, shallowly, not closely punctured, the punctures intermixed with very minute asperities on the rather strongly declivous anterior fourth; glabrous.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, the punctures small, not sharply defined; interstriae almost twice as wide as striae, the punctures small, deep, almost uniseriate. Declivity convex, steep; striae and interstitial punctures smaller than on disc, rather deep. Vestiture consisting of less than a dozen widely scattered, erect, hairlike bristles on disc and declivity, mostly on interspace 3.

Male.—Similar to female except frons convex with a slight impression above epistoma, obscurely reticulate, indistinctly punctured; striae and interstitial punctures much less clearly defined on disc and declivity.

Type Locality.—Volcan Irazu, Cartago Prov., Costa Rica.

Host.—*Oreopanax xalapense* (type), and at least two other tree species.

Type Material.—The female holotype, male allotype, and 29 paratypes were taken at the type

locality on June 28, 1963, at an elevation of 2,800 m., by S. L. Wood, from the phloem of *Oreopanax xalapense* branches. Other paratypes taken at the same locality by the same collector include: 32 taken July 13, 1963, from an unidentified branch; 38 taken October 26, 1963, from the boles of *Oreopanax nubigenus* and also from another tree, at an elevation of 2,300 m.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (s. str.) cecropicolens, n. sp.

In size and proportions this species is more nearly similar to *maurus* (Blandford) than to other species known to me, but tibial and other characters are very different.

Female.—Length 2.0 mm. (paratypes 1.9-2.2 mm.), 1.9 times as long as wide; color medium brown, with marginal areas darker, paratypes range to dark brown.

Frons rather narrowly flattened below upper level of eyes, median third on lower two-thirds of flattened area rather abruptly impressed, the impression wider below and less definite; lateral margins indefinitely elevated below level of antennal insertion; surface reticulate above, subreticulate in impressed area, the punctures coarse, sparse, sharply defined but not very deep; vestiture minute, inconspicuous, a few longer hairlike setae on epistoma.

Pronotum 0.96 times as long as wide; widest at base, sides very slightly arcuate, converging slightly to the subabrupt anterolateral angles, rather narrowly rounded in front; anterior third feebly asperate; surface reticulate, the punctures rather coarse and separated by more than their own diameters, much finer anteriorly, continuing to anterior margin; vestiture minute, appearing glabrous.

Elytra 1.7 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae feebly if at all impressed, the punctures rather coarse, moderately deep; interstriae slightly more than twice as wide as striae, weakly convex, the punctures almost as large as those of striae, those on 2 and 4 confused on basal half, almost uniseriate elsewhere. Declivity convex, rather steep; the punctures of striae and interstriae smaller, shallower, and less sharply defined than on disc. Vestiture consisting of rows of short interstitial hair; very minute striae setae visible toward base of elytra.

Male.—Similar to female except frons convex, with a slight transverse impression just above epistoma.

Type Locality.—Peralta, Cartago Prov., Costa Rica.

Host.—*Cecropia* sp.

Type Material.—The female holotype, male allotype, and 26 paratypes were collected at the type locality on March 10, 1964, at an elevation of about 500 m., by S. L. Wood, from the bark of terminal ends of branches of a cut *Cecropia* tree.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (s. str.) phoebeae, n. sp.

Allied to *cecropicolens* but larger, the anterior third of pronotum entirely devoid of

asperities, and the female frons ornamented by long hair. It is much more closely related to the following species.

Female.—Length 2.4 mm. (paratypes 2.0-2.6 mm.), 2.0 times as long as wide; color dark brown.

Frons flattened from vertex to epistoma; lateral margins below level of antennal bases weakly elevated; central area on lower half impunctate, very slightly raised, marginal areas from near epistoma to vertex closely, finely punctured and ornamented by a dense brush of long yellow hair, the hair longer and more abundant above, the longest setae on vertex attaining level of antennal bases; premandibular epistomal lobe well developed.

Pronotum 0.95 times as long as wide; widest at base, the sides almost straight on basal half and converging slightly, then rounded toward the narrowly rounded anterior margin; entire surface reticulate, finely punctured, the punctures separated from one another by 2 or more times their own diameters; glabrous.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on basal half, rather narrowly rounded behind; striae not impressed, the punctures moderately coarse, not deep; interstriae about three times as wide as striae, the punctures almost as large as those of striae, confused. Declivity rather steep, convex; striae punctures slightly smaller and deeper than on disc; interstitial punctures much smaller than those of striae, almost uniseriate on 2; 10 acutely convex from base to level of base of sternum 5. Glabrous, except a few minute hairs on costal margin.

Male.—Similar to female except frons convex above, becoming irregularly flattened below, a weak transverse impression just above epistoma, glabrous.

Type Locality.—Tapanti, Cartago Prov., Costa Rica.

Host.—*Phoebea mexicana*.

Type Material.—The female holotype, male allotype, and 151 paratypes were collected at the type locality on October 24, 1963, at an elevation of 1,300 m., by S. L. Wood, from the bark and pith of a branch 5 cm. in diameter.

The holotype, allotype, and paratypes are in my collection.

Habits.—As in all other *Scolytodes* species known to me, this species is monogamous. The adult male constructs an entrance tunnel and begins a nuptial chamber. Both male and female enlarge the oval cavity to about 3-5 mm. wide and about 5-8 mm. or more long. It is entirely within the thin bark, not engraving the wood at all; only the paper-thin, smooth outermost layer of bark remains to conceal the tunnel. Eggs are scattered indiscriminantly in the chamber; the young larvae feed along the margins of the chamber through the first and second instars, enlarging it somewhat. While the young larvae feed the parent beetles bore from the phloem through the woody tissues to the large pith area. In the pith they construct a new chamber that is usually slightly larger than the first. Third instar larvae (as judged by their size) migrate to the pith

chamber where they feed until pupation occurs. Young adults may occur in pith, xylem, or phloem tissues, but most of them remain in the pith until it is entirely consumed. The branch studied was cut on September 17; most of the brood had matured by October 24.

Scolytodes (s. str.) plumeriae, n. sp.

This species is closely related to *phoebeae*, described above, but it has the pronotal surface smooth and shining, the pronotal punctures coarse, deep, and the female frontal vestiture extends higher on the vertex and is more abundant and longer.

Female.—Length 2.3 mm. (paratypes 1.9–2.7 mm.), 2.0 times as long as wide; color very dark brown, almost black.

Frons flattened from vertex to epistoma, the lateral margins feebly raised below level of antennal insertion; surface densely, rather closely punctured, the central area impunctate and very weakly elevated, the punctures decreasing in size toward this impunctate area; vestiture very fine, moderately abundant except glabrous in impunctate area, the pubescent area scarcely extending above upper level of eyes.

Pronotum 1.0 times as long as wide; sides almost straight and parallel on basal half, rather narrowly rounded in front; surface smooth and shining, with minute points and with coarse, deep, close punctures, many punctures separated by distances less than the diameter of a puncture; lateral and anterior surface somewhat wrinkled; glabrous.

Elytra 1.2 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel on basal half, rather broadly rounded behind; striae feebly impressed, the punctures small, impressed; interstriae about three times as wide as striae, the surface smooth, with minute points, the punctures almost as large as those of striae but not as deep, confused. Declivity steep, convex; striae 1 impressed, all punctures reduced in size, punctures on interstriae 1 and 2 uniseriate, the punctures lateral to striae 2 confused. Glabrous.

Male.—Similar to female except frons convex, with a transverse impression along epistoma and continuing dorsad in lateral areas to level of antennal bases; frontal punctures fine, sparse, the vestiture scanty, inconspicuous.

Type Locality.—Playa del Coco, Guanacaste Prov., Costa Rica.

Host.—*Plumeria rubra*.

Type Material.—The female holotype, male allotype, and 77 paratypes were collected at the type locality on July 11, 1966, at sea level, by S. L. Wood, from green bark of the above host. The attack and entire life cycle were completed 20 days from the date the branch was cut. Young adults destroyed the large pith region suggesting habits similar to those of *phoebeae*. A series, not included in the type series, was also collected at Rodeo, Esquintla, Guatemala, June 4, 1964, at an elevation of 150 m., by S. L. Wood, from *Plumeria* sp.

Scolytodes (s. str.) cecropiavorus, n. sp.

Closely related to *cecropii* Schedl, but it is distinguished by the distinctly impressed striae and interstitial punctures, by the shining male frons with fine punctures, and by the more widely separated female frontal carinae.

Female.—Length 1.7 mm. (paratypes 1.4–1.8 mm.), 2.2 times as long as wide; color very dark brown.

Frons flattened from vertex to epistoma, divided on lower half into almost equal thirds by a pair of prominent, subparallel, longitudinal carinae; surface finely, rather closely punctured, and punctures somewhat sparse between carinae; lateral and upper areas ornamented by a rather sparse tuft of fine, long, yellow hair.

Pronotum 1.0 times as long as wide; widest near base, the sides weakly arcuate, converging very slightly to anterior fourth, then rather narrowly rounded in front; surface reticulate, with fine, rather sparse punctures; glabrous.

Elytra 1.3 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae 1 feebly, others not at all impressed, the punctures small, shallow; interstriae almost three times as wide as striae, obscurely marked by minute points and lines, the punctures fine, obscure, uniseriate. Declivity moderately steep, convex; striae and interstitial punctures obscurely indicated. Glabrous, except for a few small setae along costal margin.

Male.—Similar to female except frons evenly, rather weakly convex, with a weak transverse impression just above epistomal process, the surface subreticulate above, subshining below, glabrous, except a few setae near epistoma.

Type Locality.—San Ignacio de Acosta, San José Prov., Costa Rica.

Host.—*Cecropia peltata*.

Type Material.—The female holotype, male allotype, and 12 paratypes were collected at the type locality on July 5, 1963, at an elevation of 1,500 m., by S. L. Wood, from leaf petioles of the above host. The tunnels were just below the epidermal layer along the main shaft of the petiole. Additional paratypes were taken in Costa Rica as follows: 17 at Rio Damitas in the Dota Mts., San José Prov., July 22, 1963, 250 m., and 4 at Rincon de Osa, Puntarenas Prov., August 11, 1966, 30 m.; all were taken from the same host by the same collector.

The holotype, allotype, and paratypes are in my collection.

Scolytodes cecropiavorus acuminatus, n. subsp.

This subspecies is identical to *cecropiavorus* Wood, described above, except that the elytral apex is strongly acuminate and the male frons is more strongly convex. The hosts and habits are the same. Intergradation between the two forms could not be demonstrated with the limited material at hand.

Type Locality.—Tapanti, Cartago Prov., Costa Rica.

Type Material.—The female holotype, male allotype, and 7 paratypes were collected at the type locality on October 24, 1963, at an elevation of 1,300 m., by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Scolytodes cecropiavorus punctifer, n. subsp.

Male.—A series of males that must represent a geographic race of *cecropiavorus* was taken from a different, undetermined species of *Cecropia*. This subspecies is of the same size and proportions as *cecropiavorus* but the elytral apex is more broadly rounded, the declivital punctures are strongly impressed, and the male frons is sparsely, minutely punctured below and shining. The habits are the same. Intergradation between the two forms could not be demonstrated from the limited material at hand.

Type Locality.—Gatun Dam, Canal Zone, Panama.

Type Material.—The male holotype and 29 paratypes were collected at the type locality on December 31, 1963, at an elevation of about 15 m., by S. L. Wood.

The holotype and paratypes are in my collection.

Scolytodes (s. str.) venustus, n. sp.

Closely related to *pseudopiceus*, described below, but the female frons more finely punctured with the pubescence more abundant and evenly distributed, and the striae not impressed, the punctures fine and shallow.

Female.—Length 1.6 mm. (paratypes 1.4-1.8 mm.), 2.8 times as long as wide; color very dark brown, almost black.

Frons flattened from upper level of eyes to epistoma (rather narrowly above); surface subreticulate and finely punctured above eyes, subshining and rather coarsely punctured on flattened area, a small, shining, impunctate, central area on lower half; epistomal lobe not evident; vestiture consisting of fine, sparse, moderately long hair.

Pronotum 1.0 times as long as wide; widest at base, sides of basal half almost straight and parallel, rather broadly rounded in front; entire surface reticulate, the punctures coarse, deep, rather close, becoming somewhat smaller in anterior area; not at all asperate anteriorly; glabrous except at sides.

Elytra 1.3 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae 1 rather strongly, others rather weakly impressed, the punctures moderately large, deep, very close; interstriae about one and one-half times as wide as striae, almost smooth, with a few fine points, the punctures more than half as large as those of striae, deep, rather close, uniseriate. Declivity steep, convex; about as on disc, except all punctures smaller. Glabrous, except for sparse, short hair on sides and marginal areas behind.

Male.—Similar to female except frons convex, reticulate, finely, sparsely punctured, subglabrous; anterior fourth of pronotum finely asperate, the punctures in this area obscured.

Type Locality.—Rodeo, Esquintla, Guatemala.

Host.—*Plumeria* sp. (type), *P. rubra* and *Ficus* sp. (paratypes).

Type Material.—The female holotype, male allotype, and 37 paratypes were collected at the type locality on June 4, 1964, at an elevation of about 200 m., by S. L. Wood, from branches of *Plumeria*; 11 paratypes bear identical data but were taken from *Ficus* branches; 30 also have identical data but were taken from an unidentified tree branch. Four paratypes were taken at Playa del Coco, Guanacaste Prov., Costa Rica, on July 11, 1966, at sea level, from *Plumeria rubra*. The beetles live in green phloem next to dying tissues or in recently cut branches. The complete life cycle can be completed in less than 20 days.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (s. str.) pseudopiceus, n. sp.

Allied to *cecropiavorus* Wood, described above, but female frons devoid of frontal carinae, the anterior area of male pronotum feebly asperate, almost smooth in female, the striae not impressed.

Female.—Length 1.7 mm. (paratypes 1.4-1.9 mm.), 2.1 times as long as wide; color very dark brown, almost black.

Frons flattened from just above upper level of eyes to epistoma, evidently feebly convex near center; rather coarsely, closely punctured; ornamented by a rather scanty brush of fine, long, hair, the distribution about uniform, except reduced or absent toward center.

Pronotum 1.04 times as long as wide; widest near base, the sides weakly arcuate, converging slightly to anterior third then rather narrowly rounded in front; summit indefinite, near middle; anterior third appearing weakly crenulate from above, but only feebly wrinkled from other aspects; surface subreticulate, rather coarsely, deeply, closely punctured from base to anterior margin; glabrous.

Elytra 1.3 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, the punctures rather fine, deep; interstriae more than twice as wide as striae, almost smooth, the punctures subequal to those of striae, in almost regular, uniseriate rows. Declivity steep, convex; striae 1 slightly impressed; all punctures smaller than on disc. Glabrous.

Male.—Similar to female except frons convex, with a slight transverse impression just above epistomal margin, the surface reticulate and sparsely, rather deeply punctured.

Type Locality.—San Isidro del General, San José Prov., Costa Rica.

Host.—*Ficus* sp.

Type Material.—The female holotype, male allotype, and 17 paratypes were collected at the type locality on December 5, 1963, at an elevation

of 1,000 m., by S. L. Wood, from phloem tissues in a small twig less than 1 cm. in diameter. The beetles apparently attack and kill small green twigs on healthy trees.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) ochromae, n. sp.

The species is allied to *swieteniae* (Blackman), although it is not closely related. It may be distinguished by interstriae 10 not extending behind level of metacoxae, by the interstriae being almost devoid of punctures and by the absence of a frontal carina.

Female.—Length 1.4 mm. (paratypes 1.3-1.5 mm.), 2.1 times as long as wide; color rather dark brown.

Frons almost flattened above to upper level of eyes, shallowly concave below, epistoma somewhat elevated; central area on upper half smooth, impunctate, remaining areas coarsely, densely, deeply punctured; lateral areas above antennal insertions and dorsad ornamented by a scanty tuft of long, yellow hair, a few scattered setae on lower third.

Pronotum 0.95 times as long as wide; widest at base, sides feebly arcuate and slightly converging anteriorly on basal two-thirds, then rather abruptly converging toward the very narrowly rounded anterior margin; summit indefinite, near middle; anterior three-fourths armed by broad, rather coarse crenulations; basal fourth subreticulate, shining; glabrous.

Elytra 1.3 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal half, obtusely angulate behind; striae 1 weakly, others not at all impressed, the punctures rather, coarse, shallow, the rows not entirely straight; interstriae almost twice as wide as striae, almost smooth, punctures not evident. Declivity steep, convex; striae 1 and possibly 2 weakly impressed, the punctures of striae and interstriae small and deeper than on disc. Vestiture consisting of sparse flattened bristles, mostly on declivity, not more than about six or seven on any one interspace. Interspace 10 acutely elevated only to level of hind coxae.

Male.—Similar to female except frons convex above level of antennal insertions, transversely impressed between that level and epistomal process, sparsely punctured.

Type Locality.—Playon, San José Prov., Costa Rica.

Host.—*Ochroma velutina*.

Type Material.—The female holotype, male allotype, and 37 paratypes were collected at the type locality on August 9, 1963, at an elevation of about 50 m., by S. L. Wood, from the bark of branches of a cut balsa tree. Little could be discerned of the habits except that eggs apparently were scattered indiscriminantly in the oval nuptial chamber.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) cedrelae, n. sp.

Very closely related to *swieteniae* (Blackman), but the frontal carina does not attain the epistomal margin in either sex, the female carina (sometimes double) begins well above the epistoma; in addition, the female of this species has the lower frons more distinctly punctured and ornamented by sparse hair; the tuft of hair on the vertex also extends ventrad to a point in line with the anterior margin of the eye, this tuft in *swieteniae* ends well above that point.

Female.—Length 1.5 mm. (paratypes 1.3-1.5 mm.), 2.2 times as long as wide; color yellowish brown, with anterior and posterior ends and elytral suture dark.

Frons flattened from vertex to epistoma; middle half between upper level of eyes bearing a low median carina of uniform height; epistomal margin and sides near antennal bases rather coarsely deeply punctured; vestiture consisting of a dense brush of long yellow hair on vertex extending downward laterally to anteromesal angle of eye; sparse hair scattered on lower area.

Pronotum 1.1 times as long as wide; sides subparallel on basal half, converging slightly to anterior fourth, then broadly rounded in front; summit indefinite, near middle; anterior half armed by numerous, close, shining, narrow crenulations; posterior half reticulate, dull, with very fine, obscure punctures, and in discal area with small, transverse, shining granules extending to base.

Elytra 1.2 times as long as wide, 1.1 times as long as pronotum; sides almost straight and parallel on slightly more than basal half, rather narrowly rounded behind; striae not impressed, the punctures moderately large, shallow; interstriae almost twice as wide as striae, almost smooth, subshining, the punctures obscure, uniseriate. Declivity steep, convex; striae 1 and possibly 2 weakly impressed, the punctures of striae and interstriae small and deeper than on disc. Vestiture consisting of a few flattened bristles on alternate odd interspaces, mostly on declivity.

Male.—Similar to female except frons convex, with a weak transverse impression just above epistoma, the surface reticulate and sparsely punctured.

Type Locality.—Rincon de Osa, Puntarenas Prov., Costa Rica.

Host.—*Cedrela mexicana*.

Type Material.—The female holotype, male allotype, and 61 paratypes were collected at the type locality on August 11, 1966, at an elevation of about 100 m., by S. L. Wood, from transverse tunnels in the phloem of large cut logs of the above host. Fragments of this species were also found in logs of two other unidentified host species.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) immanis, n. sp.

Allied to *alni*, described below, but larger, stouter, all striae punctures in rows, and the pronotal punctures smaller.

Female.—Length 3.5 mm. (paratype 3.5 mm.), 2.4 times as long as wide; color very dark brown on head, anterior half of pronotum, elytral suture and under parts, light yellowish brown on posterior half of pronotum, elytra and legs.

Frons flattened from well above upper level of eyes to epistoma with median third of lower half very feebly impressed; impressed area smooth, shining, remaining lateral and dorsal areas rather coarsely, closely, shallowly punctured; vestiture consisting of coarse, long, subplumose, yellow hair on punctured area, a majority of the setae arising above upper level of eyes, some of those on vertex almost reaching level of antennal insertion.

Pronotum 1.04 times as long as wide; sides almost straight and parallel on basal two-fifths, then arcuately converging to the rather narrowly rounded anterior margin; dorsal profile arched from base to anterior margin, the indefinite summit on basal half; minutely, closely asperate in front of summit, reticulate and minutely, rather obscurely punctured behind, glabrous except for a few small setae at anterolateral angles.

Elytra 1.5 times as long as wide, 1.9 times as long as pronotum; sides almost straight, widest near base of declivity, narrowly rounded behind; striae not impressed, the punctures fine, shallow, in definite rows; interstriae three times as wide as striae, almost smooth, the punctures smaller than those of striae, shallow, rather numerous, confused. Declivity convex, rather steep; striae 1 and perhaps interspace 2 weakly impressed on middle third. Glabrous.

Male.—Not represented in the series at hand.

Type Locality.—Villa Mills near Cerro de la Muerte, Cartago Prov., Costa Rica.

Host.—*Miconia* sp.

Type Material.—The female holotype and one female allotype were collected at the type locality on August 1, 1966, at an elevation of 3,100 m., by S. L. Wood, from a pith cavity in a seedling terminal about 2 cm. in diameter.

The holotype and paratype are in my collection.

Scolytodes (Hexacolus) alni, n. sp.

Rather closely related to *piceus* (Blandford), but larger, and striae 3-5 with punctures somewhat confused.

Female.—Length 2.4 mm. (paratypes 2.4-2.9 mm.), 2.5 times as long as wide; color dark brown.

Frons flattened from vertex to epistoma, the surface coarsely, closely punctured; upper half ornamented by a dense brush of very long hair some of which attains epistomal margin; epistomal lobe very small.

Pronotum 1.1 times as long as wide; widest near base, the sides almost straight, converging very slightly to anterior fourth, then rather narrowly rounded in front; summit near middle; anterior half finely, densely asperate; reticulate and finely, rather sparsely punctured behind; glabrous.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae feebly impressed, at least toward base, the punctures fine, distinct; interstriae at least twice as wide as striae, marked by transverse lines, the punctures almost equal in size to those of striae, confused, rather close. De-

clivity steep, convex; striae punctures smaller and deeper than on disc, the interstriae punctures distinctly smaller than those of striae. Glabrous.

Male.—Similar to female except frons convex, weakly impressed just above epistoma, the surface shining, subreticulate, with sparse, fine punctures.

Type Locality.—Volcan Irazu, Cartago Prov., Costa Rica.

Host.—*Alnus acuminata*.

Type Material.—The female holotype, male allotype, and 26 paratypes were collected at the type locality on June 28, 1963, at an elevation of 2,300 m., by S. L. Wood, from irregular tunnels in the phloem tissues in stumps of the above host. Seventeen additional paratypes bear identical data, but were taken on October 26, 1963.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) erineophilus, n. sp.

Allied to *marginatus*, described below, but the relationship is not close. It is distinguished by the stouter pronotum with the anterior margin unarmed, and by the flattened female frons with the central area glabrous.

Female.—Length 1.6 mm. (paratypes 1.4-1.6 mm.), 2.4 times as long as wide; color medium brown.

Frons feebly convex, almost flat, on a rather narrow area from just below upper level of eyes to epistomal margin; surface etched by minute, transverse lines in central half of flattened area, remainder of flattened area rather coarsely, not closely punctured; convex area above reticulate, with sparse, fine punctures; vestiture consisting of sparse, fine, long hair on punctured part of flattened area, not conspicuous.

Pronotum 1.0 times as long as wide; widest at base, the sides very feebly arcuate, almost straight, and converging anteriorly, then rather strongly, not abruptly rounded to the broadly rounded anterior margin; finely, closely asperate on anterior half, the asperities decreasing in size and density behind, continued as very fine transverse granules to basal fourth; posterior surface and spaces between asperities strongly reticulate, finely, rather sparsely punctured behind, the anterior rims of punctures granulate except on basal fourth. Vestiture sparse, inconspicuous, confined to anterior and lateral areas.

Elytra 1.5 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on basal two-thirds, narrowly rounded behind; striae not impressed, the punctures small, distinct, rather deep; interstriae about one and one-half times as wide as striae, subshining, the punctures about two-thirds as large as those of striae, uniseriate. Declivity moderately steep, convex; striae and interstriae punctures greatly reduced in depth and clarity, obscure. Vestiture rather abundant, consisting of short, fine, semirecumbent striae and interstriae hair, interstriae setae on and near declivity longer, erect, stout, somewhat flattened.

Male.—Similar to female except frons weakly convex, reticulate, finely, sparsely punctured, the frontal vestiture shorter, less abundant; a few scattered, erect, interstriae bristles on interspaces 1, 3, and 5 almost to elytral base.

Type Locality.—Tapanti, Cartago Prov., Costa Rica.

Host.—*Ficus* sp.

Type Material.—The female holotype, male allotype, and 20 paratypes were collected at the type locality on August 17, 1963, at an elevation of 1,300 m., by S. L. Wood, from the phloem of twigs less than 1 cm. in diameter of a native fig tree.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) marginatus, n. sp.

Although the relationship may be superficial, this species appears rather closely allied to *impressus* (described below) but it is easily distinguished by the posteriorly extended tenth elytral interspace, by the finer vestiture, and by the general sculpture.

Female.—Length 1.6 mm. (paratypes 1.5-1.7 mm.), 2.9 times as long as wide; body color rather light brown.

Frons broadly plano-convex from upper level of eyes to epistoma, a shining median carina beginning as a fine line near center, becoming broader and somewhat higher then ending abruptly just above epistomal margin; surface reticulate, finely, sparsely punctured, the punctures larger and deeper near margins of flattened area; vestiture confined to marginal areas, consisting of fine, rather abundant, moderately long hair.

Pronotum 1.2 times as long as wide; sides straight and parallel on basal two-thirds, evenly, rather broadly rounded in front; anterior margin armed by ten teeth; strongly declivous and asperate on anterior third, the asperities rather large and broad, many of them arranged in broken subconcentric rows; posterior area reticulate, rather coarsely, closely punctured; vestiture confined to asperate and lateral areas, disc glabrous.

Elytra 1.6 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel on basal two-thirds, rather narrowly rounded behind; striae narrowly impressed, the punctures small, shallow; interstriae about one and one-half times as wide as striae, moderately convex, smooth, the punctures small, rather sparse, some minutely subvulcanate, uniseriate. Declivity steep, convex; striae 1 rather strongly impressed, others less strongly impressed than on disc; striae and interstitial punctures somewhat finer; interspace 1 slightly elevated. Vestiture consisting of fine, erect, rather long, interstitial hair.

Anterior coxae subcontiguous.

Male.—Similar to female except frons broadly convex, coarsely, closely, deeply punctured, with a smooth, shining, slightly elevated callus on lateral fourth of epistomal margin; elytral vestiture consisting of apically flattened bristles.

Type Locality.—Dominical, Puntarenas Prov., Costa Rica.

Type Material.—The female holotype, male allotype, and 8 paratypes were collected at the type locality on December 9, 1963, at sea level, from the phloem of small twigs in a large tree.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) plicatus, n. sp.

The armed anterior pronotal margin indicates a relationship to *impressus* and *marginatus*, both described in this article. It is unique among Costa Rican species in the remarkably broad pronotal asperities, some of which may equal one-fifth of the total width of the pronotum.

Female.—Length 1.6 mm. (paratypes 1.5-1.8 mm.), 2.5 times as long as wide; color rather light brown.

Frons mostly convex, subconvexly impressed on central third, a broad, shining callus surrounding lower third of impression; surface rather finely punctured at sides and above to level well above upper level of eyes; vestiture fine, hairlike, moderately long and abundant on punctured area.

Pronotum 1.1 times as long as wide; widest at base, sides almost straight on posterior two-thirds, converging slightly anteriorly, broadly rounded in front; anterior third rather strongly declivous, the asperities rather low, sharply raised, very broad, some as much as a fourth the total width of pronotum; anterior margin armed by a continuous costa; posterior half reticulate, with fine, shallow punctures; glabrous except for a few bristles on anterior margin.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; striae 1 weakly, others not impressed, the punctures small, shallow, not sharply defined; interstriae subreticulate, almost twice as wide as striae, the punctures fine, shallow. Declivity convex, moderately steep; striae 1 narrowly impressed; all punctures smaller and somewhat deeper than on disc. Vestiture consisting of a few sparse, erect, declivital hairs on odd numbered interspaces.

Male.—Similar to female except frons convex, reticulate, with a few obscure punctures, subglabrous.

Type Locality.—Twenty-five km. southeast of Guapiles, Limón Prov., Costa Rica.

Host.—*Ficus* sp.

Type Material.—The female holotype, male allotype, and 8 paratypes were collected at the type locality on August 22, 1966, at an elevation of about 100 m., by S. L. Wood, from the phloem of the bole of a large, cut, native, fig tree.

The holotype, allotype, and paratypes are in my collection.

Scolytodes (Hexacolus) pubescens, n. sp.

This species is readily distinguished from other Central American species by the armed anterior pronotal margin and other characters, however, it does not appear to be closely allied to any of them. The punctuation and vestiture of the elytral declivity and the sculpture of the female frons serve to distinguish it.

Female.—Length 1.8 mm. (paratypes 1.5-1.8 mm.), 2.4 times as long as wide; color rather dark brown, elytra and basal half of pronotum lighter.

Frons subconvexly impressed on slightly more than median half, with a pair of shining, rather strongly elevated, longitudinal carinae at lateral margins of concavity; surface of entire frontal area except carinae

finely, closely punctate-granulate; vestiture consisting of rather coarse, moderately long setae, rather sparse in concave area, rather dense lateral to carinae and continuing above to a level slightly above upper level of eyes, not longer above.

Pronotum 1.1 times as long as wide; widest at base, the sides very weakly arcuate on basal two-thirds, rather narrowly rounded in front; rather coarsely asperate on anterior half, the asperities confused; anterior margin armed by about a dozen low teeth; posterior half shining, coarsely, closely, deeply punctured. Vestiture hairlike, moderately abundant except glabrous at center of disc.

Elytra 1.3 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae feebly if at all impressed, the punctures close, moderately large, deep; interstriae slightly wider than striae, shining, the punctures close, almost as large and as deep as those of striae. Declivity convex, steep; all punctures smaller than on disc, confused lateral to striae 2. Vestiture rather abundant, consisting of erect, short, striae hair and slightly longer interstriae hair; not conspicuously longer on declivity.

Male.—Similar to female except frons convex, reticulate, obscurely punctured, with sparse, inconspicuous, fine hair; elytral vestiture coarser and evidently more abundant.

Type Locality.—San Ignacio de Acosta, San José Prov., Costa Rica.

Type Material.—The female holotype, male allotype, and 33 paratypes were collected at the type locality on July 5, 1963, at an elevation of 1,100 m., by S. L. Wood, from phloem tissues of a new fence post taken from an undetermined tree species.

The holotype, allotype, and paratypes are in my collection.

Habits.—Except for the nuptial chamber that reached the cambium region, the tunnels of this species were confined to the region where the inner and outer bark meet. The system of parent tunnels was roughly star-shaped, with the egg tunnels tending to be transverse. About two or three females were associated with each male. They were associated with *Scolytus dimidiatus*.

Scolytodes (Hexacolus) impressus, n. sp.

This species is rather closely allied to *marginalis* Wood, described above, but is easily distinguished by the shortened elytral interspace 10, by the more finely punctured male frons, by the suppression of reticulation on the posterior half of the pronotum, by the coarser striae punctures, and by the more abundant elytral bristles.

Male.—Length 1.5 mm. (paratypes 1.3–1.7 mm.), 2.6 times as long as wide; color rather dark, reddish brown.

Frons convex except transversely impressed along epistoma; surface obscurely reticulate, subshining, with rather fine, sparse, sharp punctures except close and deep along epistoma; vestiture largely confined to epistoma.

Pronotum 1.2 times as long as wide; sides straight and parallel on basal two-thirds, rather broadly rounded in front; anterior third finely, closely asperate; posterior half subshining, obscurely reticulate toward indefinite summit, a few minute points present, the punctures coarse, close, deep, separated by less than the diameter of a puncture; vestiture obscure, on asperate and lateral areas.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae 1 moderately, others weakly impressed, the punctures coarse, deep; interstriae as wide as striae, shining, the punctures fine, some indistinct, uniseriate. Declivity convex, steep; striae, particularly 1, more strongly impressed than on disc; interspace 1 slightly elevated; the punctures not reduced in size; vestiture consisting of apically flattened, interstriae bristles on disc and declivity, the distance between rows and between bristles in a row about equal to length of a bristle.

Female.—Not represented in the material at hand.

Type Locality.—Turrialba, Cartago Prov., Costa Rica.

Type Material.—The male holotype and 28 male paratypes were collected at the type locality on March 3, 1964, at an elevation of about 600 m., by S. L. Wood, from phloem tissues of an unidentified broken limb.

The holotype and paratypes are in my collection.

Scolytodes (Hexacolus) exiguus, n. sp.

By definition this species should be placed in the subgenus *Hexacolus* due to the pronotal asperities and absence of punctures toward the anterior margin of the pronotum; however, it almost certainly is more closely related to species here placed in the subgenus *Scolytodes* (*s. str.*). Its uniformly arched pronotum, pronotal sculpture, elevated declivital interspace 9, and other characters serve to distinguish it.

Male.—Length 1.2 mm. (paratype 1.3 mm.), 2.0 times as long as wide; color very dark brown.

Frons convex, becoming somewhat flattened toward epistoma; surface shining, with small, sparse punctures above, more closely punctured below except on shining lateral margins below level of antennal insertion; vestiture very sparse except along epistomal margin.

Pronotum 1.0 times as long as wide; widest at base, sides feebly arcuate and converging on basal two-thirds, rather broadly rounded in front; dorsal profile arched from base, but more strongly declivous on anterior third; finely asperate on anterior third, punctures intermixed with asperities to anterior tenth but evidently not attaining anterior margin; posterior area shining, with very indistinct suggestion of reticulation and a few minute points, the punctures rather coarse, close, deep, separated by distances about equal to their diameters; vestiture consisting of a few bristles in asperate area.

Elytra 1.2 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal half then increasingly arcuate to the rather narrowly rounded posterior margin; basal margins marked by a

fine raised line; striae not impressed, the punctures rather large, moderately deep; interstriae about as wide as striae, shining, almost smooth, the punctures fine, shallow, uniserial. Declivity convex, moderately steep; striae moderately to weakly impressed, the punctures somewhat smaller than on disc, deep; interstriae 1 weakly elevated, 2 and 3 weakly convex, the punctures about as on disc. Vestiture consisting of erect, apically flattened, interstitial bristles of moderate length, abraded on disc of type but on both disc and declivity of paratype.

Female.—Not represented in the material at hand.

Type Locality.—San Isidro del General, San José Prov., Costa Rica.

Host.—*Ficus* sp.

Type Material.—The male holotype and one male paratype were taken at the type locality on December 5, 1963, at an elevation of 1,000 m., by S. L. Wood, from phloem tissues of a small twig of *Ficus*.

The holotype and paratype are in my collection.

Scolytodes (Hexacolus) pumilus, n. sp.

Not related to any species of this genus known to me. Interstriae 10 ends before level of metacoxae, the pronotum is equal in width and length, the slender body is 2.5 times as long as wide, and there are a few minute asperities on anterior third of the pronotum.

Female.—Length 1.5 mm. (paratypes 1.4-1.6 mm.), 2.5 times as long as wide; color rather dark brown.

Frons rather narrowly flattened from just below upper level of eyes to epistoma; surface finely reticulate-granulate, the moderately large punctures rather close, only slightly less dense at center; vestiture very fine, moderately dense, rather long.

Pronotum 1.0 times as long as wide; widest at base, converging slightly on basal two-thirds, rather broadly rounded in front; dorsal profile arched from base, more strongly declivous on anterior third; asperities small, confused; posterior area reticulate, with very fine, sparse punctures; glabrous.

Elytra 1.5 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, the punctures rather coarse, deep; interstriae almost smooth, about as wide as striae, the punctures indefinite or absent on basal half, small, uniserial, becoming distinct toward declivity. Declivity rather steep, narrowly convex, striae 1 weakly impressed; striae punctures smaller than on disc, deep; interstriae shining, the punctures rather small, deep. Glabrous.

Male.—Similar to female except frons rather weakly convex, surface almost smooth and shining, reticulation obscurely indicated, the punctures minute, obscure; striae somewhat confused on basal fourth, interstitial punctures more evident on 1 and 2.

Type Locality.—Volcan Poas, Heredia Prov., Costa Rica.

Hosts.—*Conostegia oerstediana*, *Drimys granadensis* and *Sapium thelocarpum* (paratypes).

Type Material.—The female holotype, male allotype, and 12 paratypes were collected just

below the summit (about 100 m. below) of Volcan Poas, on August 19, 1966, by S. L. Wood, from phloem tissues of an unidentified broken tree branch. The following additional paratypes were also taken in Costa Rica during 1963, by S. L. Wood: 22 from 10 km. southeast of Cartago, Cartago Prov., July 3, at 1,800 m., from the above species of *Conostegia* and *Drimys*; and 24 from the type locality on July 14, from the above species of *Sapium*.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes acacicolens, n. sp.

This species is closely allied to *spinatus* Wood, but is readily distinguished in the male by the much smaller declivital spines, by the unaltered sculpture and vestiture of the elytral declivity, both are essentially continuous with that of the disc. In the female the pronotum is more coarsely reticulate and the elytral declivity more coarsely punctured than in *spinatus*, evidently with very fine granules on interspace 3.

Male.—Length 1.1 mm. (male paratypes 1.0-1.2; female paratypes 1.1-1.3 mm.), 2.4 times as long as wide; color light brown.

Frons convex above, transversely impressed above epistoma; surface coarsely reticulate; vestiture consisting of scattered, rather short, subplumose hair.

Pronotum 1.0 times as long as wide; subcircular, with a slight constriction on anterior half; anterior margin armed by six irregular teeth; summit at middle, high; coarsely asperate in front; posterior area rather coarsely reticulate, the punctures fine, inconspicuous; vestiture rather abundant, consisting of suberect slender scales and shorter hair intermixed.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly, evenly rounded behind; striae not impressed, the punctures moderately large, rather deep; interstriae as wide as striae, 1 and to a lesser extent 5 bearing a uniserial row of moderately large, low tubercles, the punctures on other interspaces weakly if at all granulate. Declivity convex, very slightly flattened on upper half; striae as on disc but evidently somewhat narrower; interspace 2 bearing a slender spine at upper margin of declivity, and a similar spine one-fourth of declivital length from upper margin; the spines similar in position and shape to those of *spinatus* but only half as long; interspace 5 bearing two similar but smaller spines, one just above and one just below level of lower spine on interspace 2; granules on 2 and 5 not continued below lower spine on each interspace. Vestiture consisting of fine striae hair and interstitial scales; each scale about four times as long as wide on disc and sides, somewhat shorter on striae 1-3 on lower two-thirds of declivity.

Female.—Similar to male except larger, more slender; frons a little less strongly convex; anterior margin of pronotum unarmed; declivity more strongly convex, unarmed; elytral scales more slender, somewhat shorter and narrower on declivity.

Type Locality.—Playa del Coco, Guanacaste Prov., Costa Rica.

Host.—*Acacia* sp.

Type Material.—The male holotype, female allotype, and 66 paratypes were collected at the type locality on March 21, 1967, at 10 m. elevation, by S. L. Wood, from the bark of the above host (spines slender).

Pseudothysanoes vallatus, n. sp.

This remarkable species is entirely unique in the genus. Presumably it is allied to *lecontei* Blackman, but the male declivital interstriae 3 are exceedingly strongly elevated and very coarsely serrate, the height of the elevation exceeds the combined widths of interstriae 1 and 2, 1 is neither elevated nor serrate, the elevation is only moderately developed, in the female.

Male.—Length 1.1 mm. (female paratypes 1.0-1.3 mm.), 2.7 times as long as wide; color very dark brown.

Frons convex, a slight transverse impression just above epistoma; surface rather coarsely reticulate except almost smooth on epistomal area; vestiture rather sparse, moderately long, consisting of subplumose setae. Scape short, only slightly longer but distinctly wider than pedicel, club small, oval, two weakly arcuate sutures indicated by setae.

Pronotum subcircular in outline, anterior margin armed by two subcontiguous teeth; anterior slope asperate, summit at middle; posterior area transversely subtrigose-reticulate with a few very small granules, more regularly reticulate laterally; vestiture consisting of rather sparse, slender scales and hair of equal length intermixed.

Elytra 1.7 times as long as wide, 1.8 times as long as pronotum; sides almost straight and parallel on basal two-thirds, then rounded to meet broadly truncate apex; striae not impressed, the punctures small, distinct; interstriae slightly narrower than striae, each bearing a uniseriate row of small, rounded squamiferous granules. Declivity rather steep; flattened to weakly excavated between the very strongly, very narrowly elevated interstriae 3, 1 feebly elevated toward apex, the punctures of striae 1 and 2 more strongly impressed than on disc; interstriae 3 elevated to sutural apex, armed by 10 very coarse, contiguous, blunt teeth that increase in size to just below middle of declivity; interstriae 1-9 each bearing one to three rounded nodules at base of declivity, those on 7 largest. Vestiture consisting of rows of interstitial scales and smaller striae hair; the scales longer on declivity, particularly those on summit of elevated crest of interstriae 3.

Female.—Similar to male except frons weakly impressed to upper level of eyes and more finely sculptured; scape slightly larger and bearing a small tuft of hair; anterior margin of pronotum unarmed; declivital interstriae 3 only moderately elevated and unarmed, the nodules at base of declivity also absent.

Type Locality.—Volcan Colima, Jalisco, Mexico.

Host.—*Struthanthus venetus*.

Type Material.—The male holotype, female allotype, and 12 female paratypes were taken at the type locality on June 23, 1965, 2,500 m., No. 105, from the above host, by S. L. Wood. The specimens were intermixed with *Micracisella*

and another *Pseudothysanoes*. It is presumed they mined in the cambium region.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanthoes vesculus, n. sp.

This species is closely related to *heliura* Wood, but it is easily distinguished by the smaller size, by the more slender form, by the non-elevated apical margin of the male declivity, and by the excavated female frons that bears a tuft of minute setae toward the vertex.

Male.—Length 1.1 mm. (female paratypes 0.9-1.1 mm.), 2.4 times as long as wide, color brown.

Frons not visible. Antennal scape long; sutures on club largely obsolete.

Pronotum 0.97 times as long as wide; widest near base, sides weakly arcuate, converging slightly before the broadly rounded, unarmed anterior margin; summit distinct, asperate on anterior slope, subshining, minutely, obscurely punctured and with obscure lines behind; vestiture with scales and short stout hair intermixed.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides straight, increasing very slightly posteriorly to obliquely truncate declivity; striae not impressed the punctures distinctly impressed; interstriae wider than striae, the punctures uniseriate, fine, obscure. Declivity obliquely truncate, the face evenly, weakly convex, an acutely elevated ridge extending from suture above around margin of declivity about three-fourths the distance to sutural apex, obsolete on this final fourth; striae and interstitial punctures equal in size, very close, moderately deep over entire face. Vestiture consisting of rows of interstitial scales and short striae hair; scales on disc about three times as long as wide, increasing slightly in length toward declivity; declivital margin bearing a ring of closely set, much larger, stout scales; scales on declivital face uniform in size, much smaller and more slender than on disc.

Female.—Similar to male except frons shallowly, broadly concave from epistoma to vertex, the median third of upper half densely pilose; striae punctures finer; declivity convex, without elevated margin, the sculpture essentially as on disc but slightly deeper; vestiture as on disc and somewhat finer.

Type Locality.—Three km. west of Armeria, Colima, Mexico.

Type Material.—The male holotype, female allotype, and four female paratypes were collected on June 28, 1965, 70 m., No. 131, by S. L. Wood, from a branch of an unidentified thorn tree.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes mancus, n. sp.

This species is very closely related to *spinura* Wood, but it is distinguished in the male by the steeper elytral declivity, with the circumdeclivital elevated costa higher and more acute particularly on the upper half, and, in the female, by the very deeply excavated frons.

Male.—Length 1.0 mm. (paratypes 1.0-1.2 mm.), 2.4 times as long as wide; color dark brown.

Frons as in *spinura* except impression slightly deeper.

Pronotum 0.97 times as long as wide, otherwise as in *spinura*.

Elytra evidently 1.5 times as long as wide, as in *spinura* except declivity slightly steeper, the circumdeclivital costa more strongly, subacutely elevated from sutural margin above to sutural margin below; spine-like setae on declivital interstriae 1 six in number and at least as large; vestiture similar.

Female.—As in the female of *spinura* except frons very deeply excavated on median three-fourths from epistoma to vertex, the deepest point at upper level of eyes; general surface of elytral declivity more irregular.

Type Locality.—Three km. east of Armeria, Colima, Mexico.

Type Material.—The male holotype, female allotype, and 34 paratypes were collected at the type locality on June 28, 1965, 70 m., No. 131, by S. L. Wood from the cut limb of an unidentified thorn tree. The tunnels were in the cambium region.

The holotype, allotype, and paratypes are in my collection.

Pseudothyasanoes viscivorus, n. sp.

This species is closely allied to *phorodendri* Blackman, but it may be distinguished by the larger size, by the deeper, coarser male stria punctures, by the more broadly rounded male declivity, and by the larger interstitial granules on the disc.

Male.—Length 1.7 mm. (paratypes 1.4-1.7 mm.), 2.3 times as long as wide; color dark brown to black, summit of pronotum reddish.

Frons convex, transversely impressed on lower half, subconcave toward center; surface finely reticulate-granulate, with small, obscure punctures; vestiture of sparse, subplumose setae of moderate length.

Pronotum 0.91 times as long as wide; widest on basal third, sides strongly arcuate on basal half, strongly constricted one-third length from the narrowly rounded anterior margin; anterior margin armed by six small teeth; summit behind middle, well developed; anterior slope coarsely asperate to summit; posterior area coarsely reticulate, the fine punctures obscure; vestiture of intermixed fine hair and slightly longer, erect scales, each scale about four to six times as long as wide.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae very weakly impressed toward declivity, the punctures rather coarse, deep; interstriae almost as wide as striae, the punctures uniseriate, rather coarse, subgranulate on anterior margins especially toward declivity. Declivity beginning slightly in front of middle, moderately steep, broadly convex; striae weakly impressed, the punctures slightly larger than on disc; interstitial punctures usually not at all granulate. Vestiture consisting of minute stria hair and rows of interstitial scales; each scale on disc slightly shorter than distance between rows, each about three to four times as long as wide; scales on declivity equal in width to those on disc, but three times as long; scales on declivital interstriae 8 and 9 in partial double rows and equal in length to one another.

Female.—Similar to male except anterior margin of pronotum unarmed; elytra 1.5 times as long as wide, the declivity restricted to posterior third, more narrowly rounded and steeper; stria punctures smaller, similar on disc and declivity; interstitial granules larger and more regular; declivital vestiture only slightly longer than on disc, each declivital scale about four to six times as long as wide.

Type Locality.—Volcan Ceboruco, Nayarit, Mexico.

Host.—*Phoradendron* probably *robinsonii*.

Type Material.—The male holotype, female allotype, and 17 paratypes were collected at the type locality on July 5, 1965, about 1,100 m., No. 191, by S. L. Wood, from phloem galleries in branches of the above mistletoe.

The holotype, allotype, and paratypes are in my collection.

Pseudothyasanoes amassius, n. sp.

This species is distinguished, with some difficulty, from *viscivorus* Wood, described above, and it eventually may become a subspecies. It is distinguished by a slightly more strongly impressed frons, by the shorter, uniseriate scales on the male declivital interspace 9 and a reduced number of scales on 8, and by the much broader interstitial scales of the female.

Male.—Length 1.5 mm. (paratypes 1.3-1.6 mm.), 2.1 times as long as wide; color dark brown to black, summit of pronotum reddish.

As in *viscivorus* except frons more broadly, more deeply impressed; stria punctures near declivity somewhat finer, interstitial granules finer; scales on declivital interstriae 9 uniseriate and distinctly shorter than those on 8.

Female.—As in the female of *viscivorus* except frons broadly, more strongly impressed; interstitial granules much smaller; interstitial scales much broader, each about two to two and one-half times as long as wide.

Type Locality.—Twenty km. south of Matías Romero, Oaxaca, Mexico.

Host.—*Phoradendron* sp.

Type Material.—The male holotype, female allotype, and 10 paratypes were collected at the type locality on June 24, 1967, near 700 m., No. 93, by S. L. Wood, from tunnels in the phloem of a common mistletoe that awaits identification.

The holotype, allotype, and paratypes are in my collection.

Pseudothyasanoes viscolens, n. sp.

This species clearly is allied to *viscivorus* Wood, but it is easily distinguished by the broader elytral scales which decrease in length on the lower half of the declivity, by the broadly concave female frons that bears a fringe of moderately long, yellow hair on the upper margin, and by the reduced female stria punctures.

Male.—Length 1.3 mm. (paratypes 1.3-1.7 mm.). 2.2 times as long as wide; color dark brown to black, pronotal summit reddish.

Frons (partly concealed in type) convex with a feeble impression above epistoma; an obscure subfoveate impression indicated near center; reticulate below, becoming minutely subgranulate above; vestiture sparse, inconspicuous.

Pronotum 0.92 times as long as wide; sides weakly arcuate, converging very slightly on basal two-thirds then broadly rounded in front; anterior margin armed by six small teeth; summit well developed; posterior area minutely rugulose, with sparse, small, subgranulate punctures; vestiture consisting of rather sparse, small, scale- and hair-like setae.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, the punctures rather small, deep; interstriae wider than striae, the punctures small, uniseriate. Declivity beginning well before middle of elytra, moderately steep, broadly convex; sutural striae only feebly impressed, the punctures distinctly larger and deeper than on disc; interstriae narrower, otherwise as on disc. Vestiture consisting of minute stria hair, and rows of erect interstitial scales; each scale on disc about twice as long as wide, about two-thirds as long as distance between rows; each scale on declivity as wide or slightly wider than those on disc and on upper half at least three times longer than those on disc, decreasing in length on interstriae 1 and 2 on lower half to size of scales on disc.

Female.—Similar to male except frons rather deeply concave from epistoma to vertex, the concavity clothed with moderately abundant, short, stout setae, the upper margin bearing a tuft of long yellow hair equal in length to half diameter of concavity; anterior margin of pronotum unarmed; declivity confined to posterior third of elytra; stria punctures somewhat reduced; interstitial granules small, regularly placed on disc and declivity; declivity more narrowly convex, the sculpture and vestiture as on disc, each scale three to four times as long as wide.

Type Locality.—Zamorano, Morazan, Honduras.

Host.—*Phoradendron robustissimum*.

Type Material.—The male holotype, female allotype, and 14 paratypes were collected at the type locality on April 18, 1964, 700 m., No. 569, by S. L. Wood, from tunnels in the phloem of the above named mistletoe.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes furvus, n. sp.

Among previously described species this one is more similar to *phoradendri* Blackman than to any other. It may be distinguished by the smaller size, by the more strongly convex, less strongly tuberculate elytral declivity and, in the male, by the much shorter, wider bristles on the elytral declivity.

Male.—Length 1.25 mm. (paratypes: males 1.1-1.3, females 1.2-1.4 mm.). 2.2 times as long as wide; color black with white scales.

Frons convex above, transversely impressed from just above level of antennal bases to epistomal margin; surface finely granulate; vestiture consisting of moderately abundant, coarse, short, subplumose hair.

Pronotum 0.93 times as long as wide; widest about one-third from base, sides rather strongly arcuate on basal half, laterally constricted on anterior half, narrowly rounded in front; anterior margin armed by eight serrations that decrease in size laterally; summit just behind middle, rather high; coarsely asperate from summit forward; posterior area minutely punctulate-subgranulate and with obscure, fine punctures, more nearly reticulate laterally; vestiture of minute hair and longer, broad scales, those on asperate area longer.

Elytra 1.3 times as long as wide; 1.5 times as long as pronotum; sides straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, the punctures small, deep; interstriae almost twice as wide as striae, minutely irregular, the subvulcanate, squamiferous punctures low, almost as large as those of striae. Declivity convex, steep; sculpture about as on disc but punctures and granules somewhat smaller. Vestiture consisting of interstitial rows of erect scales; each scale as long as distance between rows and between adjacent scales in the same row, about three times as long as wide.

Female.—Similar to male except slightly larger, more slender, 2.8 times as long as wide; frons less coarsely sculptured, the vestiture more abundant, finer; antennal scape bearing a small tuft of subplumose hair; sculpture of pronotum finer, the anterior margin unarmed; elytral punctures and granules greatly reduced except only slightly receded on declivity; elytral scales smaller.

Type Locality.—Finca La Pacífica, Cañas, Guanacaste Prov., Costa Rica.

Host.—*Phoradendron* sp.

Type Material.—The male holotype, female allotype, and 28 paratypes were collected at the type locality on April 13, 1966, at an elevation of about 50 m., by S. L. Wood, from stems of a mistletoe that grew in an unidentifiable cut tree. Forty-two additional paratypes were taken 20 km. southeast of Liberia on the Pan-American Highway, Guanacaste Prov., Costa Rica, on July 10, 1966, by S. L. Wood, from apparently the same species of mistletoe that grew in oak trees. A series not included in the type series was also collected at Zamorano, Morazan, Honduras, on April 18, 1964, at 700 m., by S. L. Wood, from *Phoradendron robustissimum*.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes furvatus, n. sp.

This species is very closely related to *furvus* Wood, described above, but it may be distinguished by the much coarser and deeper male stria punctures, this difference only slight in the female, by the larger, closer, interstitial granules on the male disc, and by the slightly longer, more slender male declivital scales, the female declivital scales are more slender but slightly shorter.

Male.—Length 1.2 mm. (paratypes 1.0-1.4 mm.), 2.3 times as long as wide; color dark brown to black, with summit of pronotum reddish.

Frons and pronotum as in *furvus*.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, the punctures moderately large, deep; interstriae slightly narrower than striae, smooth, each with a uniseriate row of rather small, rounded, squamiferous granules, each granule as wide as interstriae. Declivity beginning at or just behind middle, rather steep, convex; sculpture as on disc except granules smaller, many obscure. Vestiture consisting of rows of erect interstitial scales, each scale on disc two to three times as long as wide, each equal in length at base to two-thirds distance between rows, equal to distance between rows at base of declivity; each scale on declivity about four to six times as long as wide and slightly longer than distance between rows.

Female.—As in female of *furvus* except as noted in the diagnosis above.

Type Locality.—Thirty-five km. north of Juchitlan, Jalisco, Mexico.

Host.—*Phoradendron* sp.

Type Material.—The male holotype, female allotype, and 31 paratypes were collected at the type locality on July 3, 1965, about 1,300 m., No. 183, by S. L. Wood, from tunnels in the phloem of mistletoe.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes verdicus, n. sp.

This species is not closely related to any described species. The concave female frons that is ornamented by a tuft of long hair as in *viscicolens* Wood, described above, might suggest a relationship. This species differs from *viscicolens* by the more slender body form, by the elytral vestiture of the male resembling that of the female, and by the female frons being more broadly, evenly concave and ornamented by much longer setae.

Male.—Length 1.5 mm. (paratypes 1.3-1.8 mm.), 2.3 times as long as wide, color dark brown, pronotal summit reddish.

Frons convex above, moderately, transversely impressed just above epistoma with a slight impression toward center; surface finely, rugulose; vestiture sparse, rather short, widely distributed.

Pronotum 0.92 times as long as wide; widest at base, sides weakly arcuate and converging on basal three-fifths to a conspicuous constriction, rather narrowly rounded in front; anterior margin armed by four small teeth; summit rather high, behind middle; posterior area coarsely reticulate, with small, sparse, rounded, squamiferous granules; vestiture of intermixed fine, short hair and longer, slender scales.

Elytra 1.4 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, the punctures minute, distinct; interstriae about twice as wide as striae, irregularly marked by lines

and obscure points, the punctures finely granulate, squamiferous. Declivity confined to posterior third, convex, rather steep; sculpture as on disc except granules smaller, obscure. Vestiture consisting of minute striae hair and rows of erect interstitial scales; each scale on declivity four to five times as long as wide, about equal in length to distance between rows, very slightly shorter on idsc.

Female.—Similar to male except frons shallowly concave almost from eye to eye from epistoma to vertex, the upper margin ornamented by a dense tuft of long yellow hair reaching slightly beyond middle of concavity; scape with a small tuft of hair; anterior margin of pronotum unarmed; elytral scales slightly smaller.

Type Locality.—Seven km. north of Tlaxco, Tlascal, Mexico.

Type Material.—The male holotype, female allotype, and 54 paratypes were collected at the type locality on June 6, 1967, 2700 m., No. 24, by S. L. Wood, from tunnels in the phloem of a large mistletoe, awaiting identification, that grew in *Juniperus deppeana*. Thirteen additional paratypes were taken 42 km. southeast of Nochistlan, Oaxaca, Mexico, June 17, 1967, No. 55, by S. L. Wood, from *Phoradendron* sp.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes funebris, n. sp.

This species is allied to *verdicus* Wood, described above, but it is distinguished by the much smaller concavity of the female frons and absence of the frontal tuft of hair, by the larger elytral granules, particularly in the male, and by the longer, more slender elytral bristles.

Male.—Length 1.4 mm. (paratypes 1.4-1.8 mm.) 2.4 times as long as wide; color black, summit of pronotum reddish.

Frons transversely impressed below upper level of eyes, the central area shallowly concave; finely granulate-punctate above eyes, finely punctured below; vestiture consisting of moderately abundant, subplumose setae of moderate length.

Pronotum 0.95 times as long as wide; outline and sculpture as in *verdicus* except granules in posterior area reduced and setae finer.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; outline as in *verdicus*; striae not impressed, the punctures moderately large, shallow, distinct; interstriae wider than striae, surface somewhat irregularly marked by lines, the punctures fine, uniseriate, becoming granulate near declivity. Declivity confined to posterior third, rather steep, convex; striae punctures greatly reduced above, obsolete below; interstriae 1 devoid of granules on lower three-fourths and 2 on lower half, upper half of 2, all of 3 and 4 and lateral areas armed by moderately large, somewhat pointed, isolated, squamiferous granules. Vestiture consisting of erect scales; each scale on disc about four times as long as wide, almost equal in length to distance between rows, more slender, one and one-half times as long and more widely spaced than on disc; spacing of scales within row on declivity slightly greater than spacing between rows.

Female.—Similar to male except frontal concavity slightly deeper and wider; anterior margin of pronotum

unarmed; elytra 1.7 times as long as wide, the surface somewhat more irregular; elytral declivity sculptured to apex as on disc; interstitial scales about six times as long as wide, not longer or more widely spaced on declivity.

Type Locality.—Twenty-seven km. west of Durango, Durango, Mexico.

Host.—*Phoradendron villosum*.

Type Material.—The male holotype, female allotype, and 41 paratypes were collected on June 4, 1965, about 2,000 m., No. 12, by S. L. Wood, from tunnels in the phloem of the above named mistletoe.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes peniculus, n. sp.

This species is rather closely allied to *funebri* Wood, described above, but it is readily distinguished, in the male, by the continuation of all rows of interstitial scales to their normal termination on the declivity, and in the female, by the more extensively concave frons that is ornamented above by a very long tuft of yellow hair.

Male.—Length 1.4 mm. (paratypes 1.4-1.7 mm.), 2.3 times as long as wide; color dark brown, part of elytra and summit of pronotum lighter in some specimens.

Frons rather strongly, broadly, transversely impressed on lower half, convex above, the epistoma gradually raised to margin; surface finely granulate-punctate, finer in impression; vestiture consisting of moderately abundant, short, subplumose setae.

Pronotum 0.96 times as long as wide; outline as in *verdicus*; surface behind summit rather coarsely reticulate, the minute, sparse punctures obscure; vestiture of scales and stout hair intermixed.

Elytra 1.4 times as long as wide, 1.5 times as long as pronotum; outline as in *verdicus*; striae not impressed, the punctures small, shallow, obscure; interstriae about as wide as striae, irregularly marked, the punctures fine, obscure, very feebly granulate, squamiferous. Declivity on slightly more than posterior third, convex, moderately steep; sculpture essentially as on disc. Vestiture of rows of erect scales, each about four times as long as wide at base, at least eight times as long as wide on declivity, each slightly longer than distance between rows at base, increasing in length toward declivity until about twice as long as distance between rows on declivity, the spacing within each row equal to or slightly less than length of scale.

Female.—Similar to male except frons concave from eye to eye, from epistoma to vertex, area above eyes ornamented by a dense brush of long, yellow hair some of which extends to epistomal margin; scape with a rather large fringe of long hair; anterior margin of pronotum unarmed; elytra 1.6 times as long as wide, declivity confined to posterior third; elytral surface, particularly on declivity, more nearly minutely rugulose; elytral scales shorter (about two-thirds as large) and closer.

Type Material.—Thirteen km. west of Texmelucan, Puebla, Mexico.

Host.—*Phoradendron* sp.

Type Material.—The male holotype, female

allotype, and nine paratypes were collected at the type locality on June 13, 1967, 2,600 m., No. 26, by S. L. Wood, from tunnels in the phloem of the above mistletoe.

The holotype allotype, and paratypes are in my collection.

Pseudothysanoes bullatus, n. sp.

This species is rather closely allied to *peniculus* Wood, described above, but it is easily distinguished, in the male, by the presence of a rather large bulla on the lower half of declivital interstriae 3 and by the broader elytral scales, and, in the female, by the shallowly concave frons with very short hair above.

Male.—Length 1.5 mm. (paratypes 1.5-2.0 mm.), 2.3 times as long as wide; color very dark brown, posterior half of elytra usually lighter.

Frons moderately, transversely impressed on lower half, convex above; surface rather coarsely punctate-granulate above, finely rugulose on lower third; vestiture consisting of stout, rather sparse, short, subplumose setae. Scape with about a dozen long setae.

Pronotum 0.94 times as long as wide; widest at base, the sides arcuately converging from base to narrowly rounded anterior margin, with a slight constriction one-third from anterior margin; anterior margin armed by six small teeth; summit behind middle, well developed, broad; posterior area very finely rugulose-reticulate, the minute punctures obscure; vestiture of scales and hair intermixed.

Elytra 1.4 times as long as wide, 1.6 times as long as pronotum; outline as in *verdicus*; striae not impressed, the punctures rather small distinctly impressed; interstriae wider than striae, minutely, irregularly marked by obscure lines and points, the squamiferous punctures rather fine, usually distinct, not granulate. Declivity occupying slightly more than posterior third, convex, rather steep; striae and interstitial punctures reduced, becoming obsolete by middle of declivity; points largely replace obscure lines on interstriae, the surface shining; interstriae 3 with a large, low bulla on upper part of lower half of declivity, extending slightly to interstriae 2 and 4. Vestiture consisting of erect, interstitial scales, each about two to three times as long as wide, slightly longer toward declivity, those on upper declivity spaced within and between rows by a distance equal to length of a scale; lower two-thirds of declivity glabrous.

Female.—Similar to male except frons shallowly concave on median three-fourths from epistoma to above upper level of eyes, the upper area bearing rather numerous, moderately short, yellow setae; anterior margin of pronotum unarmed and more broadly rounded; declivital interstriae each bearing a uniseriate row of fine granules to apex, the bulla obscure; declivity shorter, steeper; vestiture more abundant, extending to apex, each scale more slender, about five times as long as wide.

Type Locality.—Forty-two km. southeast of Nochixtlan, Oaxaca, Mexico.

Host.—*Phoradendron* sp.

Type Material.—The male holotype, female allotype, and nine paratypes were collected at the type locality on June 17, 1967, about 2,300 m., No. 55, by S. L. Wood, from tunnels in the

phloem of the above mistletoe.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes plumalis, n. sp.

This species evidently belongs to the *verdicus* Wood, described above, group of species, although it is not closely related to any of those treated here. The female frons is feebly concave and not ornamented by long hair; the scape bears a large tuft of hair. The male elytral sculpture is simple and quite unlike related species.

Male.—Length 1.4 mm. (paratypes 1.4-1.7 mm.). 2.4 times as long as wide; color dark brown.

Frons shallowly concave almost to upper level of eyes, convex above; surface rugose-reticulate with a few fine granules in convex area; vestiture sparse, inconspicuous. Scape with fewer than a dozen setae.

Pronotum 0.91 times as long as wide; outline as in *verdicus*; posterior area reticulate, the very fine punctures obscure; vestiture of fine and stout hairlike setae.

Elytra 1.4 times as long as wide, 1.65 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, the punctures rather coarse, deep; interstriae narrower than striae, almost smooth, the punctures very fine, uniseriate. Declivity largely confined to posterior third, convex, steep; striae punctures greatly reduced, the interstitial punctures very finely granulate. Vestiture consisting of rows of small, erect, interstitial scales of about equal size on disc and declivity; each scale about three times as long as wide, about one-half as long as distance between rows of scales, spaced within rows by distances equal to about three times length of a scale.

Female.—Similar to male except frons more broadly, somewhat more deeply concave; scape bearing a large, dense tuft of long, yellow hair; pronotum armed by two teeth on anterior margin; declivity slightly shorter and steeper; declivital interstitial granules obsolete.

Type Locality.—Eighteen km. north of Huajuapán, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 10 paratypes were collected at the type locality on June 15, 1967, 2,000 m., No. 43, by S. L. Wood, from tunnels in the phloem of an unusual mistletoe that awaits identification.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes coracinus, n. sp.

This species is very similar to *hopkinsi* Blackman, but it is distinguished, in the male, by the more nearly flattened frons, by the more weakly impressed striae punctures, and by the much broader interstitial scales. The female remains unknown.

Male.—Length 1.2 mm. (male paratypes 1.2-1.3 mm.). 2.2 times as long as wide; color almost black, pronotal summit reddish.

Frons convex above, weakly, transversely impressed just above epistoma, with a narrow impression extending dorsad to center of frons; surface rugulose-reticulate;

vestiture sparse, consisting of coarse, subplumose setae of moderate length.

Pronotum 0.84 times as long as wide; widest a third from base; sides rather strongly arcuate on basal two-thirds then weakly constricted before the rather broadly rounded anterior margin; anterior margin armed by four broad, low teeth; summit high, behind middle; posterior area reticulate, the punctures sparse, minute, obscure; vestiture of stout and slender, short, hairlike setae.

Elytra 1.3 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on slightly more than basal half, rather narrowly rounded behind; striae not impressed, the punctures rather small, distinct but not deep; interstriae about as wide as striae, the punctures uniseriate, finely granulate. Declivity on slightly less than posterior half, convex, rather steep; as on disc except striae punctures slightly smaller, the interstitial granules very slightly higher. Vestiture consisting of minute, fine, striae hair and rows of erect interstitial scales; each scale about twice as long as wide; not longer on declivity.

Type Locality.—Thirty-four km. north of Juchitán, Jalisco, Mexico.

Type Material.—The male holotype and three male paratypes were collected at the type locality on July 3, 1965, about 1,300 m., No. 182a, by S. L. Wood, from tunnels in the cambium region in twigs of an unidentified tree.

The holotype and paratypes are in my collection.

Pseudothysanoes crassinis, n. sp.

This species is allied to *hopkinsi* Blackman, but it is not closely related. It is distinguished, in the male, by the much stouter body, by the longer, more slender interstitial scales, and by the large interstitial granules, and, in the female, by the slightly impressed frons, and by the much finer elytral sculpture and smaller scales.

Male.—Length 0.9 mm. (paratypes: males 0.8-1.0 mm.; females 1.0-1.2 mm.). 2.0 times as long as wide; color black.

Frons and pronotum as in *coracinus* (above) except teeth on anterior margin of pronotum more slender, the summit higher and wider, and the posterior areas obscurely reticulate.

Elytra 1.1 times as long as wide, 1.25 times as long as pronotum; sides almost straight and parallel on basal two-thirds, broadly rounded behind; striae not impressed, the punctures obsolete; interstriae each with a uniseriate row of large tubercles, increasing in size toward declivity. Declivity beginning at middle, rather steep, convex; a few minute striae punctures obscurely indicated; interstitial granules greatly reduced on upper half, obsolete on lower half, replaced by very minute, obscure punctures. Vestiture consisting of fine, moderately long, suberect, striae hair and interstitial rows of longer, erect scales; each scale about four times as long as wide on disc, six times as long as wide on declivity; each scale as long as distance between rows on disc, slightly longer on declivity, spaced within rows by a slightly greater distance.

Female.—Similar to male except larger; 2.4 times as long as wide; frontal impression very slightly larger; anterior margin of pronotum unarmed; striae punctures obscurely visible; interstitial granules obsolete; declivity

confined to posterior third of elytra, more narrowly convex; interstitial scales slender, at least eight times as long as wide.

Type Locality.—Twenty-four km. west of Tehuantepec, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 63 paratypes were collected from the type locality on June 22, 1967, 70 m., No. 35, by S. L. Wood, from tunnels in the cambium region in the bole of a small, thornless, leguminose tree having bipinnately compound leaves.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus quercinus, n. sp.

This is the first species in this genus known to me in which the frons of male and female are equally convex; the scape is also very short and bears a large tuft of hair in the female.

Male.—Length 1.0 mm. (paratypes: male 0.8-1.1, female 1.2-1.5 mm.), 2.4 times as long as wide; color very dark brown.

Frons convex, narrowly, transversely impressed just above epistoma; rugulose-reticulate, the punctures fine; vestiture moderately abundant, conspicuous, subplumose, moderately short. Scape only slightly longer than pedicel; bearing several long setae.

Pronotum 0.81 times as long as wide; widest near middle, subcircular in outline; anterior margin armed by three small teeth (four in paratypes); summit at middle, rather high, anterior slope rather coarsely asperate; posterior area smooth, shining, the punctures sparse, very minute; vestiture consisting of stout erect hair posteriorly, of bifid scales in asperate area.

Elytra 1.6 times as long as wide, 1.9 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, the punctures of moderate size and depth; interstriae almost smooth, as wide as striae, the punctures fine, uniseriate. Declivity rather steep, convex; essentially as on disc but surface more irregular. Vestiture consisting of fine, short, striae hair and rows of erect interstitial scales; each scale one and one-half times as long as striae hair, about two-thirds as long as distance between rows, similarly spaced within each row, each scale about twice as long as wide.

Female.—Similar to male except 2.8 times as long as wide; frons as in male; scape very slightly larger, bearing a large, long tuft of hair; anterior margin of pronotum unarmed; striae punctures not as deep, more widely spaced; declivity less clearly punctured; elytral scales more closely spaced within rows, very slightly longer, each scale about four times as long as wide.

Type Locality.—Thirty-seven km. west of Durango, Durango, Mexico.

Type Material.—The male holotype, female allotype, and 32 paratypes were collected at the type locality on June 4, 1965, about 2,000 m., No. 10, by S. L. Wood, from phloem tunnels in a small, shaded-out *Quercus* branch 2 cm. in diameter.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus arbuti, n. sp.

This species is rather closely allied to *quercinus* Wood, described above, but it is distinguished by the larger, median, frontal impression, by the greatly reduced tuft of hair on the scape, by the rugulose-reticulate posterior areas on the pronotum, by the larger striae punctures, and by the longer, more slender interstitial scales.

Male.—Length 1.2 mm. (paratypes 1.0-1.3 mm., males average slightly smaller than females), 2.7 times as long as wide; color very dark brown.

Frons convex above, narrowly, rather strongly, transversely impressed just above epistoma, the impression extended slightly dorsad at center; vestiture confined to epistomal margin. Scape twice as long as pedicel, bearing about six setae; club oval very slightly longer than wide.

Pronotum 0.94 times as long as wide; essentially as in *quercinus* except posterior area minutely rugulose-reticulate, most of the punctures minutely granulate.

Elytra 1.7 times as long as wide, 1.8 times as long as pronotum; outline about as in *quercinus*; striae not impressed, the punctures rather coarse, close, not sharply impressed; interstriae as wide as striae, minutely irregular, the punctures very fine, uniseriate. Declivity steep, convex; striae punctures slightly reduced in size, interstitial punctures minutely granulate. Vestiture consisting of very fine, moderately long striae hair and slightly longer, erect interstitial scales; each scale slender, equal in length to distance between rows, slightly closer within each row, each at least eight times as long as wide.

Female.—Similar to male except 3.0 times as long as wide; upper frons bearing rather abundant short, stout setae; scape bearing about a dozen setae; anterior margin of pronotum unarmed; elytral scales a little more slender.

Type Locality.—Thirteen km. west of Texmelucan, Puebla, Mexico.

Type Material.—The male holotype, female allotype, and 34 paratypes were collected at the type locality on June 13, 1967, 2,600 m., No. 27, by S. L. Wood, from twigs of *Arbutus* sp. The tunnels were immediately below the surface.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus caritus, n. sp.

This species is allied to *arbuti* Wood, described above, but it is not closely related. It differs from *arbuti* by the less strongly convex frons which lacks a transverse impression, by the smaller, less abundant, pronotal asperities, and by the very different pronotal and elytral vestiture.

Male.—Length 1.2 mm. (paratypes 1.2-1.3 mm.), 2.7 times as long as wide; color dark brown.

Frons convex to epistomal margin, a moderately large fovea just below center; surface reticulate in marginal areas, smooth and shining on middle half, with a few scattered, small, punctures; vestiture inconspicuous. Scape elongate; club small, oval.

Pronotum 1.0 times as long as wide; widest near base, the sides very weakly arcuate, converging slightly to shallow constriction one-third pronotum length from the rather narrowly rounded anterior margin; anterior margin armed by four moderately large teeth; summit at middle, moderately high; anterior slope with fine asperities; posterior area minutely rugulose, the minute punctures obscure; vestiture slender, hairlike in both asperate and posterior areas.

Elytra 1.7 times as long as wide, 1.8 times as long as pronotum; outline as in *quercinus*; striae not impressed, the punctures fine; interstriae as wide as striae, with abundant, very minute points, the punctures very fine, obscure. Declivity steep, convex, as on disc except interstitial punctures finely granulate. Vestiture consisting of very fine long, striaal hair and erect interstitial setae; each interstitial seta on disc stout, hairlike, one and one-half times as long as striaal hair, slightly longer than distance between rows, more closely spaced within each row; interstitial setae becoming scalelike on declivity and very slightly longer, each scale at least six times as long as wide.

Female.—Similar to male except 2.9 times as long as wide; frons very weakly, transversely impressed just above epistomal margin; anterior margin of pronotum unarmed; interstitial granules on declivity very minute; interstitial setae on declivity stout but essentially hairlike.

Type Locality.—Cerro Punta, Chiriqui, Panama.

Type Material.—The male holotype, female allotype, and 10 paratypes were collected January 11, 1964, 1,800 m., No. 411, by S. L. Wood, from broken branches of an unidentified tree.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus pumilus, n. sp.

This species is rather closely allied to *subpilosus* Wood, but it may be distinguished in the male by the more slender body form, and by the much smaller striaal punctures, and, in the female, by the more deeply concave frons and by the limitation of vestiture in the frontal concavity to a narrow band on upper margin.

Male.—Length 0.8 mm. (paratypes: male 0.8-0.9, female 1.0-1.1 mm.), 2.3 times as long as wide; color yellowish brown.

Frons convex, narrowly, transversely impressed just above epistomal margin, more strongly in median area; surface shining, rather coarsely reticulate; vestiture confined to epistomal margin. Antennal club rather narrowly ovate; devoid of sutures.

Pronotum 0.90 times as long as wide; widest a third from base, sides evenly arcuate to the rather broadly rounded anterior margin; anterior margin armed by four small teeth; summit just behind middle, rather well developed; asperities on anterior slope coarse; posterior area shining, minutely rugulose-reticulate, the fine punctures obscure; vestiture largely scalelike.

Elytra 1.4 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, the punctures very small but distinct; interstriae somewhat irregular, shining, twice as wide as striae, the squamiferous punctures equal in size to those of striae

but more widely spaced. Declivity rather steep, convex; sculpture as on disc but all punctures very slightly smaller. Vestiture consisting of minute, fine, striaal hair and rows of erect, interstitial scales; each scale twice as long as striaal hair, almost as long as distance between rows, about twice as long as wide, strongly tapered toward their bases.

Female.—Similar to male except 2.5 times as long as wide; frons rather deeply concave on median two-thirds to well above eyes, with a row of stout, subplumose setae on upper margin; scape bearing a small tuft of long hair; anterior margin of pronotum unarmed; striaal punctures equal in size but less distinct; elytral scales three times as long as wide.

Type Locality.—Fifty-three km. south of Colima, Colima, Mexico.

Type Material.—The male holotype, female allotype, and 56 paratypes were collected at the type locality on June 27, 1965, about 700 m., No. 122, by S. L. Wood, from an unidentified desert shrub.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus mendicus, n. sp.

This species is closely allied to *pumilus* Wood, described above, but it may be distinguished by the smoother elytral surface, by the much more slender elytral scales, and, in the female, by the less strongly concave frons that is devoid of special setal ornamentation.

Male.—Length 0.9 mm. (paratypes: male 0.9-1.0, females 1.1-1.3 mm.), 2.4 times as long as wide; color yellowish brown, some specimens darker.

Frons as in *pumilus*; pronotum also as in *pumilus* except six teeth on anterior margin larger, the posterior area more finely reticulate.

Elytra 1.4 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, narrowly rounded behind; striae not impressed, the fine punctures spaced by two diameters of a puncture; interstriae shining, marked by irregular lines, twice as wide as striae, the punctures distinctly smaller than those of striae. Declivity rather steep, convex; essentially as on disc except punctures much smaller. Vestiture consisting of very minute striaal hair and rows of erect interstitial scales; each scale three times as long as striaal hair, slightly shorter than distance between rows of scales, each about three times as long as wide.

Female.—Similar to male except 2.9 times as long as wide; frons concave on median two-thirds to upper level of eyes, not specially ornamented by setae; scape bearing a small tuft of long hair; anterior margin of pronotum unarmed; elytral punctures much more obscure; elytral scales more slender, each about six times as long as wide.

Type Locality.—Eleven km. south of Colima, Colima, Mexico.

Type Material.—The male holotype, female allotype, and 72 paratypes were collected at the type locality on June 28, 1965, about 1,000 m., No. 120, by S. L. Wood, from an unidentified thornless, leguminous, desert, shrubby tree. Additional paratypes were taken in Mexico as follows: 19 at 3 km. W. Armeria, Colima, June

28, 1965, 70 m., No. 137, S. L. Wood; and 17 at 24 km. W. Tehuatepec, Oaxaca, June 22, 1967, 70 m., No. 85, S. L. Wood; presumably all taken from the same host species.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus acares, n. sp.

This species is rather closely related to *mendicus* Wood, described above, but it is distinguished by the larger size, by the more irregular, more deeply punctured elytra, and by the larger, more closely spaced interstitial scales.

Male.—Length 1.2 mm. (paratypes: males, 1.1-1.2, females 1.3-1.4 mm.), 2.2 times as long as wide; color yellowish brown, the elytra darker.

Frons and pronotum as in *mendicus*, except posterior area of pronotum almost smooth and shining.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; outline about as in *mendicus*; striae not impressed, the punctures rather coarse; interstriae as wide as striae, the punctures rather large, uniseriate. Declivity steep, convex; sculpture about as on disc except interstitial punctures closer. Vestiture consisting of minute striaal hair and rows of erect interstitial scales; each scale two-thirds as long as distance between rows, similarly spaced within rows; each scale twice as long as wide.

Female.—Similar to female of *mendicus* except 2.7 times as long as wide; frons somewhat more deeply impressed, with a few minute granules in upper third of impression; striaal and interstitial punctures closer and more distinct, the general surface more irregular; declivity much more coarsely, deeply punctured; interstitial scales much closer, each four to six times as long as wide, very slightly longer.

Type Locality.—Thirty km. southeast of El Cameron, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 25 paratypes were collected at the type locality on June 21, 1967, near 1,000 m., No. 80, by S. L. Wood, from the branch of an unidentified tree (probably leguminose).

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus aquilus, n. sp.

This species is allied to *mendicus* Wood, described above, but it may be distinguished by the slightly larger size, by the darker color, by the much more broadly rounded anterior margin of the pronotum, by the much coarser male striaal punctures, by the much more coarsely punctured female elytral declivity, and by the more extensive female frontal impression.

Male.—Length 1.1 mm. (female paratypes 1.2-1.4 mm.), 2.3 times as long as wide; color dark brown.

Frons and pronotum as in *mendicus* except anterior margin of pronotum much more broadly rounded, bearing eight teeth, and posterior area more clearly punctured.

Elytra 1.4 times as long as wide, 2.1 times as long as pronotum; outline as in *mendicus*; striae not impressed, the punctures rather coarse, round, deep, interstriae as

wide as striae, almost smooth, the punctures minute, uniseriate. Declivity rather steep, convex; striaal punctures decreasing rapidly in size, almost obsolete at apex; interstitial punctures minute. Vestiture consisting of fine, minute, striaal hair and rows of erect interstitial scales; each scale almost as long as distance between rows, each about four times as long as wide.

Female.—Similar to male except 2.7 times as long as wide; frons shallowly concave from epistoma to vertex, smooth and shining on median half below, not specially ornamented by setae; anterior margin of pronotum unarmed; elytral surface more irregular, the striaal punctures smaller, but distinct; interstitial punctures minute, mostly obscure; declivity more irregular, more coarsely punctured much as in *acares*; interstitial scales more closely placed.

Type Locality.—Twenty-six km. east of Morelia, Michoacan, Mexico.

Type Material.—The male holotype, female allotype, and 21 female paratypes were collected at the type locality on June 14, 1965, 2,500 m., No. 56, by S. L. Wood, from phloem tunnels in an *Acacia* branch.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus mirus, n. sp.

This species is rather closely related to *acares* Wood, described above, but it may be distinguished by the more deeply impressed female frons above, by the more coarsely sculptured posterior areas of the pronotum, and by the much finer declivital punctures.

Male.—Length 1.0 mm. (paratypes: male 1.0-1.1, female 1.2-1.4 mm.), 2.2 times as long as wide; color yellowish brown.

Frons similar to *acares* but more strongly convex. Pronotum as in *acares* except reticulation in posterior areas tending to be very slightly more rugulose.

Elytra 1.3 times as long as wide, 1.4 times as long as pronotum; outline as in *acares*; striae not impressed, the punctures rather coarse, more sharply impressed than in *acares*; interstriae irregular but much smoother than in *acares*, as wide as striae, the punctures rather small and more widely spaced than in *acares*. Declivity steep, convex; surface smoother, the punctures very slightly smaller than on disc. Vestiture as in *acares* except interstitial scales very slightly more widely spaced.

Female.—Similar to female of *acares* except 2.8 times as long as wide; frons more abruptly impressed at upper limits of concavity; posterior areas of pronotum more strongly reticulate; elytral surface less rugulose; declivital punctures reduced to very fine striaal and interstitial punctures; elytral scales similar, but less abundant.

Type Locality.—Thirty-eight km. south of Matías Romero, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 40 paratypes were collected at the type locality on June 24, 1967, 250 m., No. 92, by S. L. Wood, from branches 1 to 5 cm. in diameter of a leguminose shrub having a yellow, mimosa-like flower.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus obesus, n. sp.

Apparently this species is more closely allied to *columbianus* Blackman than to other known species, but it is distinguished by the stouter body, shorter antennal scape; and by the less closely placed interstitial scales.

Male.—Length 1.0 mm. (paratypes: male 1.0-1.2, female 1.2-1.4 mm.), 2.0 times as long as wide; color reddish brown, the elytra black (lighter in less mature specimens).

Frons planoconvex almost to upper level of eyes; minutely punctate above, becoming smoother below; vestiture consisting of a few short subplumose setae over flattened area. Scape short, little longer than pedicel, bearing a small tuft of hair; club moderately large, oval.

Pronotum 0.86 times as long as wide; widest one-third from base, sides rather strongly arcuate converging toward the narrowly rounded anterior margin; anterior margin armed by four teeth, the median pair larger; summit behind middle, well developed; anterior area coarsely asperate; posterior area very minutely rugulose, the punctures obscure; vestiture largely scalelike.

Elytra 1.15 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on slightly more than basal half, rather broadly rounded behind; striae not impressed, the punctures small, obscure, interstriae wider than striae, the punctures fine, uniseriate. Declivity steep, broadly convex; surface minutely rugulose, as on disc except interstitial punctures closer. Vestiture consisting of interstitial rows of erect scales, each scale less than twice as long as wide.

Female.—Similar to male except 2.3 times as long as wide; frons shallowly concave to upper level of eyes; scape larger, broadly triangular, bearing a large tuft of long hair; anterior margin of pronotum unarmed; elytra minutely rugulose, all punctures obscure.

Type Locality.—Thirty km. southeast of El Cameron, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and 26 paratypes were collected at the type locality on June 21, 1967, near 1,000 m., No. 79, by S. L. Wood, from twigs of a tree awaiting identification.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus excavatus, n. sp.

This remarkable species is unique in the genus. It is distinguished by the remarkably extensive frontal excavation of both sexes; its larger size and the short, tufted scape also aid in distinguishing it.

Male.—Length 1.4 mm. (paratypes: male 1.6, female 1.4-1.6 mm.), 2.1 times as long as wide; color dark brown to black.

Frons very broadly, deeply, concavely excavated from eye to eye, from epistoma to vertex, the upper margin acute with median fourth projecting cephalad slightly; surface reticulate, glabrous. Mandibles near middle armed by a transverse, strongly developed ridge. Antennal scape slightly longer and twice as wide as pedicel; club twice as long as wide.

Pronotum 0.89 times as long as wide; widest two-fifths from base, the sides and anterior margin equally rounded on an almost circular arc; anterior margin armed by two small teeth; summit at middle, broad; anterior slope very coarsely asperate; posterior areas almost smooth, obscurely reticulate, shining; small scales almost obsolete except at margins.

Elytra 1.2 times as long as wide, 1.4 times as long as pronotum; widest at base, the sides straight on basal two-thirds, very feebly converging posteriorly, broadly rounded behind; striae not impressed, the punctures small, shallow, somewhat obscure; interstriae wider than striae, minutely subrugulose, shining, the punctures fine, obscure. Declivity steep, convex; striae punctures greatly reduced, becoming obsolete; interstitial punctures finely granulate. Vestiture consisting of minute, fine, striae hair and rows of erect interstitial scales; each scale on disc slender, elongate, slightly longer than distance between rows, becoming shorter but not narrower toward declivity, on declivity each scale equal in length to little more than half distance between rows, about twice as long as wide. Posterior margin of sternum 5 narrowly rounded, projecting slightly.

Female.—Similar to male except 2.3 times as long as wide; frontal excavation slightly deeper with median area near epistoma slightly elevated; mandibular ridge absent; scape wider, bearing a small tuft of hair; margin of pronotum unarmed; discal scales on elytra slightly shorter; sternum 5 less strongly produced.

Type Locality.—Thirty km. southeast of El Cameron, Oaxaca, Mexico.

Type Material.—The male holotype, female allotype, and three paratypes were collected at the type locality on June 21, 1967, near 1,000 m., No. 78, by S. L. Wood, from the twigs of the same tree that harbored the preceding species, *obesus*.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus spicatus, n. sp.

This species and the next one form a new species group within the genus. They differ from all representatives of the genus in having the last visible male abdominal tergum very narrow, produced medially into a projecting mucro; in the female a similar projecting mucro is formed by the last visible sternum; the female frons is also concave.

Male.—Length 1.7 mm. (paratypes 1.5-1.8 mm.), 2.4 times as long as wide; color dark brown, summit of pronotum reddish brown.

Frons convex above, becoming more nearly flattened on lower third; surface rugulose-reticulate and obscurely punctured; an indefinite, median, subfoveate impression just below upper level of eyes; vestiture fine, short, inconspicuous except long and conspicuous along epistomal margin. Scape elongate.

Pronotum 0.90 times as long as wide; widest a third from base, sides arcuate, a weak constriction on anterior third, rather broadly rounded in front; anterior margin armed by about eight small teeth; summit just behind middle, moderately high; asperities on anterior slope rather large; posterior area rugulose-reticulate, a few fine granules behind summit; vestiture hairlike.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, the punctures very small, obscure; interstriae almost twice as wide as striae, very finely rugulose, the punctures very fine, their anterior margins very finely granulate. Declivity convex, steep; sculpture essentially as on disc. Vestiture consisting of fine, moderately long stria hair and rows of slightly longer interstitial bristles; each bristle about two-thirds as long as distance separating rows, separated within rows by distances equal to length of bristle, bristles becoming scalelike on declivity, each scale there at least three times as long as wide. Last visible tergum narrowly produced into a mucro-like process that projects beyond elytral apex.

Female.—Similar to male except 2.6 times as long as wide; frons shallowly concave to vertex, lower, median half smooth, shining and ascending toward epistomal margin; anterior margin of pronotum unarmed; interstitial setae on disc fine, hairlike, bristlelike on declivity; mucro formed by last visible sternum; last tergum rounded on posterior margin.

Type Locality.—Cerro Punta, Chiriqui, Panama.

Type Material.—The male holotype, female allotype, and 48 paratypes were collected at the type locality on January 11, 1964, 1,800 m., No. 382, from cambium tunnels in an unidentified log about 1 m. in diameter.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus subulatus, n. sp.

This species is rather closely related to *spicatus* Wood, described above, but it may be distinguished by the much larger and deeper stria punctures, by the longer, broader, elytral scales, and by the much more strongly impressed female frons.

Male.—Length 1.4 mm. (paratypes 1.3-1.7 mm.), 2.3 times as long as wide; color very dark brown to black, pronotal summit reddish brown.

Frons and pronotum as in *spicatus* except part of pronotal vestiture stout.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; outline as in *spicatus*; striae not impressed, the punctures rather large, deep, sharply impressed; interstriae almost smooth, shining, one and one-half times as wide as striae, the uniseriate punctures finely granulate. Declivity steep, convex; striae very feebly impressed, the punctures more obscure. Vestiture consisting of short, fine stria hair (some flattened on declivity), and rows of longer, interstitial scales; each scale slightly more than half as long as distance between rows, separated within rows by distances equal to length of scale, each about twice as long as wide. Tergal mucro about as in *spicatus*.

Female.—Similar to male except 2.6 times as long as wide; frons rather deeply concave on median three-fourths from epistoma to vertex, a small, smooth, median area on lower half, most females ornamented by a small, sparse tuft of hair at upper margin of concavity; anterior margin of pronotum unarmed; stria punctures not as deep, perhaps smaller; interstitial scales very slightly longer and more slender, each scale about four times as long as wide; tergal mucro replaced by sternal mucro as in *spicatus*.

Type Locality.—Volcan Pacaya, Esquintla, Guatemala.

Type Material.—The male holotype, female allotype, and 57 paratypes were collected at the type locality on June 1, 1964, 1,300 m., No. 700, by S. L. Wood, in tunnels in the phloem of branches less than 8 cm. in diameter of a tree named Caldo de Frijol by a local woodcutter. The local host name obviously was derived from the odor of freshly cut wood.

The holotype, allotype, and paratypes are in my collection.

Cryptulocleptus mucronatus, n. sp.

While most of the generic characters of *Cryptulocleptus* clearly fit this species, it is unique in having the elytral apices acuminate extended to form a short mucro as seen in *Micracis* or possibly *Micracisella*. The mucro appears to be a secondary acquisition that should not have a bearing on the generic placement of this species.

Male.—Length 1.3 mm. (paratypes 1.2-1.4 mm.), 2.5 times as long as wide; color dark reddish brown.

Frons convex, with a feeble impression just above epistoma; surface rather coarsely rugulose above, more finely below, with a small, median, smooth area on lower third; vestiture short, sparse. Scape elongate, with fewer than a dozen setae; club broadly oval, unmarked by any indication of sutures.

Pronotum 1.0 times as long as wide; widest two-fifths from base, the sides weakly arcuate, moderately constricted a fourth of pronotum length behind the broadly rounded anterior margin; anterior margin armed by four minute teeth; summit at middle, moderately high; anterior slope armed by many small asperities; posterior areas rather coarsely reticulate, with moderately abundant, fine, isolated granules behind summit; vestiture of stout, hairlike setae.

Elytra 1.5 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind except for the very short, sutural mucro; striae not impressed, the punctures fine, distinct; interstriae minutely subrugulose, wider than striae, the punctures small, obscure, becoming granulate toward declivity. Declivity convex, very steep; stria punctures larger than on disc but very obscure; interstitial punctures replaced by rather large rounded granules. Vestiture consisting of very fine, moderately long stria hair and rows of erect interstitial scales; the scales slightly shorter and more slender on disc; each scale on declivity spaced within and between rows by distance equal to length of scale, each about four times as long as wide. Apex with a very short mucro.

Female.—Similar to male except 2.6 times as long as wide; frons less strongly convex, less coarsely rugulose, with median fovea near center; anterior margin of pronotum unarmed; elytral scales more slender, at least six times as long as wide on declivity.

Type Locality.—La Lima, Cortez, Honduras.

Type Material.—The male holotype, female allotype, and 14 paratypes were collected on May 5, 1964, 70 m., No. 572, by S. L. Wood, from tunnels in the xylem of stems 1 cm. in diameter from an unidentified shrubby, woody vine.

The holotype, allotype, and paratypes are in my collection.

Thysanoes neotropicalis, n. sp.

This species is more closely related to *mexicanus* Wood than to others in the genus, but it is larger, more slender, more finely striate, and it has the female frons more strongly impressed. This is the first species of *Thysanoes* reported south of Mexico.

Female.—Length 2.1 mm. (paratypes: females 2.0-2.2, males 1.5-1.9 mm.), 3.2 times as long as wide; color medium brown, pronotum lighter on type (only).

Frons broadly, somewhat transversely impressed from epistoma to upper level of eyes, the central area more narrowly impressed, subfoveate; epistomal area smooth and shining to subfoveate impression, sides and above finely, obscurely punctured and finely, closely, subaciculate granulate; vestiture inconspicuous. Tuft of setae on scape much smaller than in *mexicanus*.

Pronotum 1.2 times as long as wide; slightly wider near middle, the sides straight and diverging on basal half, converging slightly anteriorly toward the broadly rounded subserrate anterior margin; summit almost one-third from anterior margin; posterior area reticulate and very finely punctured; vestiture confined to marginal areas consisting of flattened bristles.

Elytra 2.1 times as long as wide 1.8 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, the punctures small, shallow; interstriae about twice as wide as striae, subshining, irregular but not clearly marked by lines or punctures. Declivity convex, steep; surface dull, striae punctures smaller than on disc, perhaps deeper; interstriae with occasional fine granules. Vestiture confined to declivity, consisting of erect interstitial scales with an additional, partial row at suture; each scale three to four times as long as wide.

Male.—Similar to female except smaller, 1.8 mm., stouter, 26 times as long as wide; frons less extensively impressed; anterior margin of pronotum armed by ten serrations; elytra with striae punctures much larger and deeper, the interstitial punctures uniseriate granulate toward declivity, both striae punctures and moderately large interstitial granules continuing to apex of declivity; declivital vestiture longer and extending well onto disc.

Type Locality.—San Ignacio de Acosta, San José Prov., Costa Rica.

Host.—*Calliandra confusa*.

Type Material.—The female holotype, male allotype, and 22 paratypes were collected at the type locality on July 5, 1963, at an elevation of 1,500 m., by S. L. Wood, from dying branches of the above host. The tunnels were in the wood as in other species of the genus.

The holotype, allotype, and paratypes are in my collection.

Thysanoes subsulcatus, n. sp.

This species is allied to *fimbraticornis* LeConte, but it is distinguished by the larger size, by the more deeply impressed female frons, by the rather large interstitial declivital granules,

and by the much longer, more slender declivital scales.

Female.—Length 2.2 mm. (paratypes 1.9-2.3 mm.), 3.0 times as long as wide; color dark reddish brown.

Frons shallowly, broadly concave from epistoma to vertex, with a small, median impression near upper level of eyes; surface strongly reticulate, almost subrugulose, except transversely etched on a rather large area above epistomal margin; vestiture short, stout, sparse, uniformly distributed. Scape with a small fringe of hair.

Pronotum 1.2 times as long as wide; sides straight and parallel on slightly less than basal two-thirds, very broadly rounded in front, anterior margin unarmed; summit well in front of middle, broad; surface strongly reticulate, the punctures minute, very leebly granulate behind summit; vestiture fine, hairlike in posterior areas, stout bristles in asperate areas.

Elytra 2.0 times as long as wide, 1.9 times as long as pronotum; sides straight and parallel on slightly more than basal two-thirds, broadly rounded behind; striae not impressed, the punctures very fine, shallow, distinct; interstriae more than twice as wide as striae, minutely irregular, the punctures fine, obscure. Declivity steep, convex; striae punctures almost obsolete; interstriae 2 slightly elevated, each interstriae uniseriate, rather finely granulate, except punctures and granules obsolete on lower three-fourths of 1. Vestiture consisting of very minute, fine, striae hair, and uniseriate rows of longer, erect, interstitial scales; each scale on disc about half as long as distance between rows and three times as long as wide, on declivity slightly longer than distance between rows and up to six times as long as wide, obsolete on middle half of declivital interstriae 1.

Male.—Similar to female except frontal concavity deeper, extending only to upper level of eyes; anterior margin of pronotum armed by eight small teeth; discal striae punctures slightly larger, interstitial punctures granulate on posterior third; declivital granules much larger; declivital scales slightly wider and longer.

Type Locality.—Eight km. west of Tulancingo, Hidalgo, Mexico.

Type Material.—The female holotype, male allotype, and eight paratypes were collected at the type locality on June 11, 1967, 2,400 m., by S. L. Wood, from *Quercus* branches.

The holotype, allotype, and paratypes are in my collection.

Thysanoes epicharis, n. sp.

This species is allied to *fimbraticornis* LeConte, but it is distinguished by the less deeply impressed, more strongly reticulate female frons, by the more coarsely sculptured elytral disc, by the almost obsolete declivital striae, and by the much broader scales on the elytral declivity.

Female.—Length 1.2 mm. (paratypes 1.8-2.2 mm.), 3.0 times as long as wide; color yellowish brown.

Frons rather strongly, transversely impressed from epistomal margin to well above eyes, a small median impression just below center; entire surface rather strongly rugulose-reticulate; vestiture fine, short, sparse. Scape bearing a rather dense fringe of long hair.

Pronotum 1.08 times as long as wide; sides almost straight and parallel on basal half, distinctly constricted on anterior half, broadly rounded in front; anterior

margin unarmed; summit in front of middle; posterior area reticulate, the punctures moderately abundant, rather small, shallow; vestiture of fine hair and stout bristles, rather short.

Elytra 1.8 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on basal three-fourths, broadly rounded behind; striae not impressed, the punctures small, distinct; interstriae twice as wide as striae, irregularly subruglose, the punctures small, obscure. Declivity convex, steep, confined to posterior fourth; striae very weakly impressed, the punctures minute, distinct; interstriae almost smooth, with very fine, uniseriate, squamiferous granules, those on 3 very slightly larger. Vestiture of minute strial hair and uniseriate rows of erect interstitial scales; each scale on disc half as long as distance between rows, three times as long as wide; declivital scales three-fourths as long as distance between rows, two to three times as long as wide; a partial supplemental row along suture.

Male.—Similar to female except frontal impression reduced, not reaching upper level of eyes, the central impression more pronounced, sculpture of upper half granulate; anterior margin of pronotum armed by six teeth; declivital granules very slightly larger.

Type Locality.—Twenty-four km. south of Mazamitla, Jalisco, Mexico.

Type Material.—The female holotype, male allotype, and eight paratypes were collected at the type locality on June 22, 1965, 2,500 m., by S. L. Wood, from branches of a leguminose tree.

The holotype, allotype, and paratypes are in my collection.

Thysanoes adonis, n. sp.

This species is allied to *mexicanus* Wood, but it is distinguished by the larger size, by the subfoveate frons, by the absence of interstitial granules on basal half of disc, and by longer and much more slender interstitial declivital scales.

Female.—Length 2.0 mm. (paratypes 1.4-1.9 mm.), 2.6 times as long as wide; color dark brown, summit of pronotum reddish brown.

Frons convex above, transversely impressed on lower half of area below upper level of eyes, a small median, sublobrate impression at center, ascending toward epistomal margin; surface densely, minutely, evidently subruglosely punctured in convex area, becoming almost smooth toward epistoma; vestiture of sparse, moderately long, very stout bristles uniformly distributed on convex area. Scape bearing about a dozen long hairs.

Pronotum 1.04 times as long as wide; sides almost straight and parallel on basal half, moderately constricted on anterior half, rather broadly rounded in front; anterior margin subseriate; summit at middle, rather broad; asperities on anterior slope rather coarse; posterior areas reticulate, the punctures minute, sparse, a few behind summit minutely granulate; vestiture of stout bristles.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal three-fourths, rather broadly rounded behind; striae not impressed, the punctures small, distinct; interstriae about three times as wide as striae, the surface irregular, subrugulose, the punctures small, uniseriate, finely granulate on posterior half. Declivity convex, steep, restricted to posterior fourth; strial punctures obsolete, except some of them very finely granulate; interstriae uniseriately, finely granulate; general surface somewhat dull. Vestiture of

very minute strial hair, and uniseriate rows of much longer, interstitial scales; each scale on disc about two-thirds as long as distance between rows, about four times as longer as wide; scales on declivity slightly longer than distance between rows, about six times as long as wide, with a smaller supplemental row at suture.

Male.—Similar to female except anterior margin of pronotum more distinctly serrate; elytral granules smaller, the declivital strial punctures minute but visible; declivital scales broader, about four to five times as long as wide.

Type Locality.—Twenty-nine km. west of Quiroga, Michoacan, Mexico.

Type Material.—The female holotype, male allotype, and seven damaged paratypes were collected at the type locality on June 17, 1965, 2,200 m., by S. L. Wood, from *Quercus* branches.

The holotype, allotype, and paratypes are in my collection.

Micracisella monadis, n. sp.

This species is perhaps more closely allied to *hondurensis* Wood than to other known species, but it is easily distinguished by the very different frontal sculpture, by the rows of rounded interstitial granules on the declivity, and by the distinctly elevated declivital interstriae 9.

Female.—Length 1.7 mm. (paratypes 1.5-1.7 mm.), 2.9 times as long as wide; color dark brown.

Frons planoconvex from epistoma to well above eyes, the epistomal margin slightly elevated toward center; surface very minutely, longitudinally etched, approaching reticulation laterally; glabrous. Scape more than three times as long as pedicel, broad, bearing a large tuft of hair.

Pronotum 1.1 times as long as wide; widest at middle, sides weakly arcuate on posterior two-thirds, weakly constricted on anterior third before the rather narrowly rounded anterior margin; anterior margin armed by two basally contiguous, small teeth; summit at middle broad; posterior areas coarsely reticulate with a few minute granules near and behind summit; a few scales on marginal areas.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on more than basal two-thirds, narrowly rounded behind; striae not impressed, the punctures very small, distinct; interstriae marked by lines, shining, three times as wide as striae, the punctures fine, obscure. Declivity convex, rather steep; strial punctures larger, deeper, very obscure; interstitial punctures replaced by small rounded granules. Apex of elytra subacuminate. Vestiture consisting of very short, fine, strial hair and rows of longer, erect, interstitial scales; each scale slightly shorter than distance between rows, similarly spaced within rows, each scale about four times as long as wide, gradually, strongly narrowed toward their bases.

Male.—Similar to female except frons convex, a narrow, transverse impression just above epistoma, the surface finely rugose-reticulate, a few short, stout setae in lateral areas; tuft of hair on scape smaller; scape more slender; teeth on anterior margin of pronotum larger; declivital scales very slightly wider.

Type Locality.—Volcan Colima, Jalisco, Mexico.

Host.—*Struthanthus venetus*.

Type Material.—The holotype, allotype, and seven paratypes were collected at the type locality on June 23, 1965, 2,500 m., No. 105, by S. L. Wood, from axial pith tunnels in twigs of the above named mistletoe.

The holotype, allotype, and paratypes are in my collection.

Micracisella scitula, n. sp.

This species is allied to *monadis* Wood, described above, but it is readily distinguished by the strongly convex frons, by the smaller, less numerous declivital interstitial granules, by the wider declivital scales, and by the presence of four teeth on the anterior margin of the pronotum.

Male.—Length 1.6 mm., 3.0 times as long as wide; color reddish brown.

Frons rather strongly convex, with a narrow, transverse impression just above epistomal margin; surface rather coarsely reticulate except almost smooth on small median area on lower half, a few very small granules scattered on upper half; vestiture sparse, very short in convex area, longer below.

Pronotum 1.2 times as long as wide; widest near middle, the sides very feebly arcuate, almost parallel on more than basal half, rather narrowly rounded in front; anterior margin armed by four small teeth, median pair slightly larger; summit broad, near middle; posterior area coarsely reticulate, a few shining points evidently represent obsolete punctures; vestiture reduced to a few very stout bristles in marginal areas.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on slightly more than basal two-thirds, rather broadly rounded behind except subacuminate at suture; striae not impressed, the punctures small, distinct, anterior margins of some of them very feebly elevated; interstriae shining, subrugulose, the punctures two-thirds as large as those of striae, shallow, some obscure. Declivity convex, rather steep; striae punctures somewhat obscure; interstitial punctures on upper half replaced by rounded granules; subreticulate toward suture near apex. Vestiture largely abraded on disc of type, evidently shorter than on declivity; on declivity consisting of rows of erect, interstitial scales, each scale almost as long as distance between rows, more widely spaced within each row except on 1, each scale broad, averaging about twice as long as wide. Apex acuminate, the mucro short; not at all divaricate.

Type Locality.—Fourteen km. east of Huatusco, Veracruz, Mexico.

Type Material.—The male holotype was collected at the type locality on July 7, 1967, near 1,300 m., No. 173, by S. L. Wood, from *Quercus* twigs.

The holotype is in my collection.

Micracisella nitidula, n. sp.

This species is allied to *monadis* Wood, described above, but it may be distinguished by the reticulate-granulate frons, by the slender declivital interstitial scales, by the much smaller declivital interstitial granules, and by the

presence of four marginal teeth on the pronotum.

Female.—Length 1.9 mm., 3.1 times as long as wide; color black.

Frons convex, less strongly on lower half, epistomal margin weakly elevated; surface very finely reticulate-granulate, reduced to minute points on small median area near epistoma; vestiture consisting of rather sparse, conspicuous, subplumose setae of moderate length to vertex. Scape twice as long as pedicel, bearing a small tuft of hair.

Pronotum 1.1 times as long as wide; widest just behind middle, sides rather strongly arcuate, weakly constricted on anterior third, rather narrowly rounded in front; anterior margin armed by six small teeth of equal size; summit near middle, rather broad; posterior area minutely reticulate-granulate, with a few minute, almost flat, granules toward summit; vestiture rather stout, moderately abundant, rather long.

Elytra 2.0 times as long as wide, 2.0 times as long as pronotum; sides almost straight and parallel on basal three-fourths, narrowly acuminate behind; striae not impressed, the punctures small, shallow; interstriae twice as wide as striae, somewhat irregular, the punctures very fine, uniserate. Declivity convex, rather steep; striae punctures slightly deeper than on disc; interstitial punctures replaced by fine granules; apex subacuminate, mucro not developed, not at all divaricate. Vestiture consisting of very fine, moderately long striae hair and rows of erect interstitial scales, slightly longer on declivity; each scale on declivity slightly longer than distance between rows, similarly spaced within each row, each about six times as long as wide.

Type Locality.—Ten km. northeast of Tezuilán, Puebla, Mexico.

Type Material.—The female holotype was collected at the type locality on July 2, 1967, 1,600 m., No. 142, by S. L. Wood, from an axial pith tunnel in *Rubus* sp. A second female specimen, almost certainly this species but not designated as a paratype, was taken 26 km. east of Morelia, Michoacan, Mexico, June 14, 1965, 2,500 m., S. L. Wood, from an *Arbutus* sp. twig.

The holotype is in my collection.

Micracisella nigrella, n. sp.

This species is allied to *nigra* Wood, but it is distinguished by the coarser sculpture of striae punctures and declivital granules, by the larger, coarser, more abundant interstitial scales, and by the different arrangement of marginal teeth on the pronotum.

Female.—Length 1.7 mm. (paratypes 1.5-1.8 mm.), 3.0 times as long as wide; color almost black, summit of pronotum reddish brown.

Frons convex on upper half, transversely impressed on lower half, an indistinct median impression toward center; vestiture sparse, of very short, fine, subplumose setae. Scape twice as long as pedicel, bearing a moderately large tuft of long hair.

Pronotum 1.14 times as long as wide; widest just behind middle, the sides weakly arcuate on more than basal half, rather narrowly rounded in front anterior margin armed by two rather large teeth; summit at middle, rather broad; posterior area minutely reticulate-

granulate, with moderately abundant, isolated, very fine granules; vestiture of rather short, broad scales.

Elytra 1.9 times as long as wide, 1.7 times as long as pronotum; outline as in *nitidula*; striae not impressed, the punctures fine, distinct, shallow, interstriae with fine lines, twice as wide as striae, the punctures very fine, half as large as those of striae. Declivity convex, rather steep; interstitial punctures about as large as those of striae; apex acuminate, the sutural apex distinctly, shallowly emarginate. Vestiture consisting of rows of erect interstitial scales; each scale very slightly shorter than distance between rows, similarly spaced within rows, each about two and one-half to three times as long as wide; a supplemental sutural row of smaller scales on declivity.

Male.—Similar to female except frons slightly more convex; scape without tuft of hair; elytral scales very slightly larger.

Type Locality.—Volcan de Agua, Esquintla, Guatemala.

Type Material.—The female holotype, male allotype, and 81 paratypes were collected at the type locality on May 19, 1964, 1,000 m., No. 603, by S. L. Wood, from branches of an unidentified shrub somewhat resembling *Rhus*.

The holotype, allotype, and paratypes are in my collection.

Micracisella similis, n. sp.

This species is allied to *nigra* Wood, but it is distinguished by the more slender body form, by the less strongly convex frons, with a slight median impression above epistoma, and much greater development of the vestiture, and by the more strongly reticulate pronotal disc.

Female.—Length 1.5 mm. (paratypes 1.4–1.5 mm.), 3.0 times as long as wide; color black, summit of pronotum reddish brown.

Frons planoconvex, flattened toward center, gradually ascending to epistomal margin on lower fourth; surface minutely reticulate-granulate, smoother medially toward epistoma; vestiture moderately long and abundant toward lateral areas, subplumose. Scape twice as long as pedicel, bearing a small tuft of long hair.

Pronotum 1.16 times as long as wide; widest at middle, sides on basal half straight, almost parallel, rather narrowly rounded in front; anterior margin armed by two moderately large, basally contiguous teeth; summit at middle, broad; posterior areas minutely reticulate-granulate, with a few, fine scattered granules; vestiture short, scalelike.

Elytra 1.9 times as long as wide, 1.7 times as long as pronotum; outline as in *nitidula*; striae not impressed, the punctures small, shallow; interstriae marked by lines, shining, slightly less than twice as wide as striae, the uniseriate punctures very fine. Declivity convex, rather steep; striae punctures somewhat reduced; interstitial punctures replaced by fine granules on upper half, almost obsolete below; general surface granulose toward sutural apex; apex acuminate, the sutural apex shallowly emarginate. Vestiture consisting of minute, fine, striae hair and uniseriate rows of longer, erect, interstitial scales; each scale slightly shorter than distance between rows, similarly spaced within each row, each scale on declivity about three times as long as wide.

Male.—Similar to female except frons more nearly convex, the frontal vestiture somewhat shorter; reduction

of interstitial tubercles on lower half of declivity less pronounced.

Type Locality.—Volcan Ceboruco, Nayarit, Mexico.

Type Material.—The female holotype, male allotype, and seven paratypes were collected at the type locality on July 5, 1965, 1,200 m., No. 189, by S. L. Wood, from axial pith tunnels in *Serjania* sp.

The holotype, allotype, and paratypes are in my collection.

Micracisella vescula, n. sp.

This species is allied to *similis* Wood, described above, but it may be distinguished by the coarser striae punctures, by the absence of interstitial granules on the declivity, and by the large, broader, interstitial scales.

Female.—Length 1.4 mm. (allotype 1.35 mm.), 3.0 times as long as wide; color dark brown, summit of pronotum reddish brown.

Frons as in *similis* but less strongly flattened. Scape twice as long as pedicel, bearing a tuft of long hair.

Pronotum 1.17 times as long as wide; outline as in *similis*; anterior margin armed by two moderately large, subcontiguous teeth; posterior area minutely reticulate-granulate, with obscure, subgranulate punctures; vestiture of rather abundant, short scales, each twice as long as wide.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; outline as in *nitidula*; striae not impressed, the punctures rather fine, not always clearly defined; interstriae irregular, almost subrugulose, as wide as striae, the uniseriate punctures fine. Declivity convex, rather steep; striae punctures deeper than on disc, the interstitial punctures equal in size to those of striae; apex acuminate, shallowly emarginate at sutural apex. Vestiture consisting of very fine, short, striae hair and interstitial rows of erect, uniseriate scales, each scale about as long as distance between rows, similarly spaced within each row, each about three times as long as wide; a supplemental row of smaller, sutural scales on declivity.

Male.—Similar to female except frons more strongly convex, the frontal vestiture shorter; tuft of hair on scape much smaller; teeth on anterior margin of pronotum slightly larger.

Type Locality.—Two km. north of Cerro Gordo, Veracruz, Mexico.

Type Material.—The female holotype and male allotype were collected at the type locality on July 6, 1967, 1,000 m., No. 166, by S. L. Wood, in axial pith tunnels in *Serjania* sp.

The holotype and allotype are in my collection.

Micracisella squamatula, n. sp.

This species is allied to *nigra* Wood and the three preceding species, but it is easily distinguished from these and all other representatives of the genus by the much more widely spaced teeth on the anterior margin of the pronotum, by the scalelike, small, striae setae in addition to

those of the interstriae, and by the more strongly divaricate elytra at the sutural apex.

Female.—Length 1.4 mm. (paratypes 1.3–1.5 mm.), 3.0 times as long as wide; color black, summit of pronotum reddish brown, vestiture white.

Frons convex above, becoming flattened below, then ascending slightly to epistomal margin; surface reticulate-granulate above, becoming almost smooth in central area below except for a few fine points; vestiture rather abundant and long in large dorsolateral areas. Scape about twice as long and slightly wider than pedicel, bearing a small tuft of long hair.

Pronotum 1.1 times as long as wide; widest at middle, the sides on posterior half almost straight and parallel on basal half, feebly constricted on anterior third, rather narrowly rounded in front; anterior margin armed by two moderately large, rather widely separated teeth; summit at middle, rather broad; posterior area finely reticulate-granulate, with a few minute granules; vestiture consisting of short, broad scales.

Elytra 1.8 times as long as wide, 1.7 times as long as pronotum; outline as in *nitidula*; striae not impressed, the punctures small, somewhat indistinct; interstriae irregularly marked by fine points and lines, one and one-half times as wide as striae, the punctures fine, uniseriate. Declivity convex, rather steep; stria punctures evidently slightly deeper; interstitial punctures replaced by small rounded granules; sutural apex emarginate. Vestiture consisting of rows of small stria scales, each slightly longer than diameter of a stria puncture, about four times as long as wide, and rows of longer interstitial scales; each interstitial scale one and one-half times as long as stria scales and about equal in length to distance between rows of interstitial scales, each about three times as long as wide.

Male.—Similar to female except frons more strongly convex on upper two-thirds, the smooth area much smaller and subreticulate; tuft of hair on scape reduced.

Type Locality.—Ten km. south of Huajuapán, Oaxaca, Mexico.

Type Material.—The female holotype, male allotype, and nine paratypes were collected at the type locality on June 16, 1967, about 2,000 m., No. 45, by S. L. Wood, from axial pith tunnels in *Serjania* sp. Five additional paratypes were taken 32 km. south of Huajuapán, Oaxaca, Mexico, on the same date, No. 49, from twigs of an unidentified shrub.

The holotype, allotype, and paratypes are in my collection.

Micracisella divaricata, n. sp.

While several of the tropical species in this genus have the elytral apices very slightly divaricate, this character is pronounced in this species and serves to distinguish it.

Female.—Length 1.6 mm. (paratypes 1.5 mm.), 2.8 times as long as wide; color black, central area of pronotum reddish brown.

Frons planoconvex from epistoma to upper level of eyes; surface coarsely reticulate above and laterally becoming smooth toward center, the punctures fine, moderately abundant; vestiture consisting of moderately long, stout, subplumose setae moderately abundant in lateral areas and above. Scape twice as long as pedicel, bearing a small tuft of long hair.

Pronotum 1.1 times as long as wide; widest on basal half, the sides almost straight and parallel, then arcuately rounded to constriction on anterior third, narrowly rounded in front; anterior margin armed by two, rather large, basally contiguous teeth; summit rather indefinite, at middle; small asperities continue to just behind summit, isolated granules continue to base; surface of posterior area coarsely reticulate; vestiture of small, short scales.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on more than basal two-thirds, then narrowly rounded to blunt apex; striae not impressed, the punctures very small; interstriae shining, marked by lines, twice as wide as striae, the uniseriate punctures fine, somewhat obscure. Declivity convex, rather steep; stria punctures largely obsolete; interstitial punctures replaced by rounded granules; apex divaricate, the emargination as wide as width of antennal club and half as deep. Vestiture consisting of very minute, very fine stria hair and rows of longer, suberect, interstitial scales, each scale slightly shorter than distance between rows, similarly spaced within rows except closer on 1, each scale about four times as long as wide.

Male.—Similar to female except frons more strongly convex, the setae more evenly distributed; elytral scales slightly wider, about three times as long as wide.

Type Locality.—Two km. north of Cerro Gordo, Veracruz Mexico.

Type Material.—The female holotype, male allotype, and one female paratype were collected at the type locality on July 6, 1967, 1,000 m., No. 166, by S. L. Wood, from axial pith tunnels in *Serjania* sp.

The holotype, allotype, and paratype are in my collection.

Micracis costaricensis, n. sp.

The only species known to me that is at all similar to this one is *carinulatus* Wood. This species may readily be distinguished from *carinulatus* by the dull surfaces, by the more irregularly punctured elytra, by the more delicate, more strongly flattened interstitial scales, and by the slightly impressed second declivital interspace.

Female.—Length 2.7 mm. (paratypes 2.2–2.8 mm.), 3.2 times as long as wide; color rather dark reddish brown.

Frons strongly, transversely impressed and slightly concave from epistoma to well above eyes, upper half of impressed area with a fine, low median carina; surface coarsely reticulate except smooth just above epistoma; vestiture consisting of sparse, short setae in reticulate area, with a fringe of long subplumose hair along margin of impressed area above level of eyes. Scape flattened, triangular, ornamented by a fringe of long hair; sutures of club strongly procurved, 1 reaching middle, 2 extending three-fourths of club length from its base.

Pronotum 1.3 times as long as wide; widest on basal half, sides almost straight and parallel on slightly more than basal half, rather broadly rounded in front; anterior margin armed by 12 rather coarse, isolated teeth; summit in front of middle; rather coarsely reticulate behind summit with rather sparse, fine, subgranulate punctures. Vestiture consisting of rather short, stout, delicate, white setae.

Elytra 1.9 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal three-fourths, rather broadly rounded behind to the

short, projecting sutural apex; striae not impressed, the punctures small, shallow, distinct; interstriae about three times as wide as striae, irregular, punctures and other features obscured by irregular surface features. Declivity evenly convex, very steep; striae slightly impressed, the punctures deeper than on disc; interstriae weakly convex, with lower half of 2 somewhat impressed; all interspaces bearing median rows of fine, rounded granules, those in lateral areas a little larger; terminal mucro as in other species of this genus. Vestiture consisting of rows of fine stria hair and delicate, very slender interstitial scales of equal length; each scale almost equal in length to distance between rows of scales; easily abraded.

Male.—Similar to female except slightly smaller, 2.4 mm., stouter, 2.8 times as long as wide; frons convex with a slight transverse impression just above epistoma, surface finely granulate, the vestiture greatly reduced; scape not dilated, the tuft of hair almost obsolete; pronotum and elytra very slightly more coarsely sculptured.

Type Locality.—Volcan Poas, Heredia Prov., Costa Rica.

Host.—*Calliandra confusa* (paratypes).

Type Material.—The holotype, allotype, and 41 paratypes were collected at the type locality on June 19, 1966, at an elevation of about 2,000 m., by S. L. Wood, from branches of a leguminose shrub. Additional paratypes were taken in Costa Rica as follows: 18 from Tapanti, Cartago Prov., 1,400 m., Aug. 17, 1963; 25 from Santa Ana, San José Prov., 1,400 m., Oct. 4, 1963; and 3 from San Ignacio de Acosta, San José Prov., 1,500 m., July 5, 1963, all taken by S. L. Wood, from *Calliandra confusa*. Eleven specimens not included in the type series are from Zamorano, Morazan, Honduras, April 18, 1964, 700 m., from *Salix guatemalensis*.

The holotype, allotype, and paratypes are in my collection.

Micracis carinulus, n. sp.

Similar to *costaricensis* Wood, described above, but smaller, the declivital striae not impressed, the impression of the female frons not reaching upper level of eyes with the median carina rather sharply elevated.

Female.—Length 2.1 mm. (paratypes 1.6-2.1 mm.), 3.1 times as long as wide; color yellowish brown.

Frons broadly concave from epistoma to upper level of eyes, upper half divided by a fine, low carina, surface smooth and shining just above epistoma, then finely punctured and becoming coarsely reticulate on upper half; vestiture consisting of short, stout, close setae in concave area, and long, curved, subplumose hairs along upper margin of concavity. Antenna as in *costaricensis*, except wider.

Pronotum as in *costaricensis* except anterior margin unarmed.

Elytra as in *costaricensis* except surface of disc a little more irregular and stria punctures less distinct. Declivity evenly convex except for terminal mucro; stria punctures very slightly impressed; interstriae with small, rather obscure granules. Vestiture consisting of moderately long, rather abundant coarse stria and interstitial setae; those on median row of each interspace slightly longer.

Male.—Similar to female except frons convex and finely granulate with a slight transverse impression above epistoma; scape less strongly dilated; anterior margin of pronotum armed by about eight small serrations; and median rows of elytral setae more nearly scalelike.

Type Locality.—Playón, Puntarenas Prov., Costa Rica.

Host.—*Rheedia edulis*.

Type Material.—The female holotype, male allotype, and 20 paratypes were collected at the type locality on February 22, 1964, at an elevation of about 50 m., by S. L. Wood, from branches of the above host. Two additional paratypes were taken at Fort Clayton, Canal Zone, Panama, on December 22, 1963 at about 30 m., by S. L. Wood, from a fallen limb of an unidentified tree.

The holotype, allotype, and paratypes are in my collection.

Micracis tribulatus, n. sp.

This species is very closely related to *costaricensis* Wood, described above but it may be distinguished by the darker color, by the more slender form, by the armed anterior margin of the female pronotum, by the granulate, discal, interstitial punctures, and by the coarser declivital granules.

Female.—Length 2.8 mm. (paratypes 2.2-2.8 mm.), 3.6 times as long as wide; color very dark brown.

Frons and antenna as in *costaricensis*.

Pronotum 1.2 times as long as wide; sides straight and parallel on basal two-thirds, rather broadly rounded in front; anterior margin armed by six small teeth; summit distinct, in front of middle; posterior areas reticulate-granulate, with sparse, moderately large, isolated granules to base; vestiture of fine hair and slender scales.

Elytra 2.3 times as long as wide, 2.0 times as long as pronotum; sides straight and parallel on basal three-fourths, narrowly mucronate behind; stria punctures very small, distinct; interstriae at least three times as wide as striae, subshining, marked by lines, the punctures fine, subgranulate; declivity steep, convex, confined to posterior fourth; interstitial punctures replaced by moderately large, rounded granules; apex mucronate. Vestiture consisting of fine stria hair and rows of longer, erect, interstitial scales, slightly longer on declivity; each scale on disc about six to eight times as long as wide, much more slender on declivity.

Male.—Similar to female except 2.9 times as long as wide; frons convex above, transversely impressed below, with a small median impression; scape smaller, narrower; teeth on anterior margin of pronotum larger; declivital scales slightly longer.

Type Locality.—Twenty-six km. west of Texmelucan, Puebla, Mexico.

Type Material.—The female holotype, male allotype, and 9 paratypes were collected at the type locality on June 6, 1967, 2,900 m., No. 29, by S. L. Wood, from *Salix*.

The holotype, allotype, and paratypes are in my collection.

Micracis lepidus, n. sp.

This species is not closely related to any species known to me, although there may be a remote relationship to *lignator* Blackman. The size, scalelike elytral setae, armed anterior margin of the female pronotum, and the unexcavated female frons distinguish it.

Female.—Length 3.0 mm. (paratypes 2.3–3.0 mm.), 3.2 times as long as wide; color dark brown to black with white scales.

Frons convex above, somewhat flattened on lower third; surface reticulate and finely punctured above, smooth, shining on lower part of flattened area; vestiture subplumose, erect, rather abundant to vertex except on shining epistomal area, short below, moderately long above. Scape broadly triangular, ornamented by a marginal fringe of long hair; club 1.6 times as long as wide, suture 1 reaching middle.

Pronotum 1.3 times as long as wide; sides almost, straight and parallel on basal half, rather broadly rounded in front; anterior margin armed by 12 low teeth; summit in front of middle, distinct; posterior area reticulate-granulate, very minute granules indicated toward summit in median area; vestiture short, of minute hair and slender scales.

Elytra 2.0 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal three-fourths, rather narrowly mucronate behind; striae not impressed, the punctures minute; interstriae about four times as wide as striae, undulating slightly and with numerous indefinite points, the punctures fine. Declivity steep, convex, confined to posterior fourth; striae and interstitial punctures of equal size, close, confused, rows of minute granules on all interstriae except 1; apex obtusely mucronate. Vestiture consisting of minute striae hair and erect scales; scales on disc in interstitial rows, more abundant and confused on declivity, each scale three to four times as long as wide; base of declivity also with several pointed bristles longer than scales, sides with some slender, long hair.

Male.—Similar to female except averaging lightly smaller; 2.6 times as long as wide; frons more strongly convex, not flattened below, surface with many rounded granules; scape less strongly expanded, the tuft of hair smaller; teeth on anterior margin of pronotum larger; elytral scales shorter, broader, mostly twice as long as wide, the bristles and interstitial hair also scalelike and slightly larger than other scales.

Type Locality.—Cerro Punta, Chiriquí, Panama.

Type Material.—The female holotype, male allotype, and 50 paratypes were collected at the type locality on December 19, 1963 and January 11, 1964, 1,800 m., No. 315, 371, 387, 404, by S. L. Wood, from branches of *Inga* sp.

The holotype, allotype, and paratypes are in my collection.

Micracis lignicolus, n. sp.

This species is closely related to *lignator* Blackman, but it is distinguished by the less strongly elevated interstriae 9 at base of male declivity, and by the less strongly tuberculate interstriae at margin of declivity, by the slightly

elevated, subserrate, male declivital interstriae 3 on basal third, by the different arrangement of setae on the female frons and scape, and by the narrower interstitial scales in both sexes.

Male.—Length 2.8 mm. (paratypes 2.5–3.3 mm.), 2.8 times as long as wide; color reddish brown.

Frons convex above, transversely impressed on lower half, epistomal margin slightly elevated; surface reticulate-granulate, with sparse, smooth granules on convex area; vestiture sparse, limited to lateral areas. Scape about twice as long as pedicel, distal width equal to length, bearing a small tuft of long hair; club 1.8 times as long as wide, suture 1 extending three-fifths of club length from base.

Pronotum 1.1 times as long as wide; sides almost straight and parallel on basal half, weakly constricted just in front of middle, anterior margin rather broadly rounded and armed by 12 teeth; summit at middle, broad; posterior areas reticulate-granulate, the punctures fine, inconspicuous, some minutely granulate; vestiture consisting of minute hair and slender scales.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal three-fourths, narrowly rounded behind; striae moderately impressed on posterior third of disc, the punctured rather coarse and deep; interstriae as wide as striae, shining, somewhat irregular, the punctures uniseriate, rather fine. Declivity rather abrupt, convex, steep; striae not impressed, the punctures smaller and squamiferous; interstriae 1–8 each with one or two rounded nodules at base of declivity as in *lignator*, 9 weakly elevated but ending just behind base of declivity, 3 bearing a row of about six pointed tubercles on upper two-thirds, 5 bearing two similar tubercles near base; apex extended slightly but terminated by ascending costal margins that form a pseudo-emargination; interstitial punctures coarse, two-thirds as large as those of striae, squamiferous. Vestiture consisting of minute striae hair and interstitial rows of slender, erect scales on disc; on declivity striae setae and some interstitial setae form moderately short scales each about four times as long as wide, other erect, interstitial scales in rows, much longer at declivital base, some more than twice as long as ground scales.

Female.—Similar to male except 3.2 times as long as wide; frons convex to epistoma, median half glabrous, devoid of granules; scape triangularly extended, bearing a much larger tuft of hair, but shorter than in *lignator*; striae not impressed toward declivity; declivity devoid of tubercles or nodules, 3 weakly convex; vestiture less dense on declivity, the scales more slender, not longer than on disc.

Type Locality.—Cerro Peña Blanca, Honduras.

Type Material.—The male holotype, female allotype, and 13 paratypes were taken at the type locality on April 23, 1964, 2,000 m., No. 529, in *Miconia schlechtendalii*, by S. L. Wood; 23 paratypes bear identical data except lot 533 taken from branches of *Quercus williamsi*; four paratypes were from Zamorano, Morazan Honduras, April 18, 1964, 700 m., No. 539, *Quercus sapotaeifolia*, S. L. Wood; 15 paratypes were from Volcan de Agua, 1,000 m., No. 598, from an unidentified broken branch, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Micracis detentus, n. sp.

This species is very closely related to *carinulus* Wood, described above, but it may be distinguished by the larger size, by the larger granules behind the pronotal summit, by the more deeply impressed female frons with a more prominent median elevation below, and by the coarser interstitial bristles on the declivity.

Female.—Length 2.2 mm. (paratypes 1.8–2.3 mm.), 3.2 times as long as wide; color yellowish brown.

Frons transversely, subconcavely impressed from epistoma to upper level of eyes, median third of epistoma moderately elevated, the smooth, impunctate, shining elevation extending about one-third of distance to upper level of eyes; remaining surface reticulate-granulate, the punctures minute, obscure; vestiture of minute subplumose hair, becoming longer toward upper margin of impression. Scape narrowly triangular, ornamented by a tuft of long hair; club 1.7 times as long as wide, suture 1 extending slightly beyond middle.

Pronotum 1.3 times as long as wide; sides straight and parallel on slightly more than basal half, rather broadly rounded in front; anterior margin unarmed; summit in front of middle; posterior area reticulate-granulate, with rather sparse, fine, isolated granules; vestiture hairlike, inconspicuous.

Elytra 2.0 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal three-fourths, acuminate behind; striae not impressed, the punctures small, distinct; interstriae at least twice as wide as striae, with lines and points, the punctures uniseriate, very fine. Declivity steep, convex, confined to posterior fourth; minutely granulose, stria punctures deeper but somewhat obscure; interstitial punctures replaced by fine granules; apex rather strongly acuminate. Vestiture consisting of very fine stria hair and rows of erect, interstitial bristles, slightly longer and coarser on declivity; each bristle on declivity slightly longer than distance between rows.

Male.—Similar to female except 2.7 times as long as wide; frons convex above, a moderate transverse impression on lower half, the median elevation obsolete; scape not as wide as long, bearing a small tuft of shorter hair; anterior margin of pronotum armed by eight teeth; declivital vestiture slightly coarser.

Type Locality.—Twenty-four km. south of Mazamitla, Jalisco, Mexico.

Type Material.—The male holotype, female allotype, and five paratypes were collected at the type locality on June 22, 1965, 2,500 m., No. 94, by S. L. Wood, from branches of a leguminose tree; 11 paratypes were taken 8 km. south of Atenqueque, Jalisco, Mexico, on June 25, 1965, 1,000 m., No. 118, by S. L. Wood, from an unidentified shrub; two paratypes were from Maguarichic, Chihuahua, Mexico, July 13, 1960, blacklight, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Micracis unicornis, n. sp.

This species evidently is closely related to *detentus* Wood, described above, but the male bears a large, pointed median tubercle on the

epistoma, the vestiture is finer, and the elytral declivital tubercles and pronotal asperities are larger.

Male.—Length 2.1 mm. (male paratype 2.1 mm.), 2.7 times as long as wide; color reddish brown.

Frons convex above, transversely impressed on lower half; epistomal margin slightly raised, with a rather indefinite median elevation that bears a conspicuous, moderately large, pointed tubercle; surface reticulate, the punctures obscure, a few fine granules in convex area; vestiture of coarse, subplumose setae of moderate length, rather sparse. Scape twice as long and twice as wide as pedicel, bearing a small tuft of hair; club 1.55 times as long as wide, suture 1 extending slightly beyond middle of club.

Pronotum 1.05 times as long as wide; sides feebly arcuate, subparallel on basal half, rather broadly rounded in front; anterior margin armed by 12 coarse teeth; summit at middle; posterior area reticulate-granulate, with a few minute granules behind summit, the minute punctures obscure; vestiture inconspicuous, composed of stout hairlike setae.

Elytra 2.0 times as long as wide, 2.0 times as long as pronotum; sides straight and parallel on basal three-fourths, narrowly mucronate behind; striae not impressed, the punctures small, distinct; interstriae about four times as wide as striae, marked by many lines and a few points, the punctures fine, shallow. Declivity steep, convex, confined to posterior fourth; stria punctures larger and impressed; interstriae minutely granulose, the punctures replaced by fine granules. Vestiture consisting of minute stria hair and rows of erect, pointed, interstitial bristles, longer and stouter on declivity; each bristle on declivity slightly longer than distance between rows.

Type Locality.—Six km. west of Quiroga, Michoacan, Mexico.

Type Material.—The male holotype and one male paratype were collected at the type locality on June 17, 1965, 2,200 m., No. 72, by S. L. Wood, from a shrubby herbaceous plant.

The holotype and paratype are in my collection.

Micracis inimicus, n. sp.

The scalelike interstitial setae on the elytra and the armed anterior margin of the pronotum suggest a relationship to *evanescens* Wood, but this species is smaller and the frontal sculpture of the female is entirely different.

Female.—Length 2.3 mm. (paratypes 2.0–2.5 mm.), 3.5 times as long as wide; color medium to dark brown.

Frons broadly concave to upper level of eyes, lower third with unusual sculpture; epistomal margin slightly elevated, smooth on a narrow band on median fourth, then a slight, narrow ridge, then above this a narrow slit-like impression, rather strongly abruptly, transversely elevated above impression on more than median half, its upper slope marked by two or three minute, transverse ridges in its gradual descent to concavity; vestiture short, sparse, inconspicuous; surface reticulate-granulate. Scape narrowly triangular, ornamented by a tuft of long hair; club 1.9 times as long as wide, widest on distal half, suture 1 extending two-thirds of club length from base.

Pronotum 1.3 times as long as wide; as in *detentus*, except some setae stout, almost scalelike.

Elytra 2.1 times as long as wide, 1.75 times as long as pronotum; outline and disc as in *detentus* except stria punctures rather obscure. Declivity steep, convex, confined to posterior fourth; striae weakly impressed, the punctures larger, deeper; interstitial punctures subgranulate, except reduced on 2; granules larger in some paratypes. Vestiture consisting of very fine stria hair and rows of erect interstitial scales, slightly longer on declivity; each scale on declivity as long as distance between scales, spaced more closely within each row, truncate at their apices, each about five times as long as wide.

Male.—Similar to female except 2.7 times as long as wide; frons convex, transversely impressed on lower half, epistoma elevated on median third, without elaborate sculpture of female; anterior margin of pronotum armed by six teeth; declivital tubercles more distinct except on interstriae 2 and 3.

Type Locality.—Volcan de Agua, Esquintla, Guatemala.

Type Material.—The female holotype, male allotype, and 21 paratypes were collected at the type locality on May 19, 1964, 1,000 m., No. 603, by S. L. Wood, from branches of an unidentified shrub.

The holotype, allotype, and paratypes are in my collection.

Micracis festivus, n. sp.

Apparently the only known species allied to this one is *inimicus* Wood, described above, but it is easily distinguished by the slender elytral setae, and by the very different frontal sculpture of the female.

Female.—Length 2.2 mm. (paratypes 1.7-2.3 mm.), 3.4 times as long as wide; color dark brown.

Frons concavely impressed from epistoma to above upper level of eyes; epistomal margin elevated, median half with a narrow, slit-like impression just above margin and a low elevated, transverse, subcarinate ridge immediately above the slit; surface reticulate-granulate, the punctures fine, obscure; vestiture sparse, fine, short below, longer above. Scape narrowly triangular, ornamented by a tuft of long hair; club 1.6 times as long as wide, suture 1 extending beyond middle.

Pronotum 1.2 times as long as wide; as in *detentus* except granules in posterior areas larger and anterior margin armed by six small teeth.

Elytra 2.1 times as long as wide, 1.8 times as long as pronotum; outline and disc as in *detentus* except stria punctures very slightly deeper. Declivity steep, convex, confined to posterior fourth; striae feebly impressed, the punctures deeper and slightly larger than on disc; interstriae each armed by a row of rounded granules similar to but slightly larger than in *inimicus*; apex strongly acuminate or mucronate. Vestiture consisting of fine stria hair and rows of longer interstitial bristles, slightly longer on declivity; each bristle up to one and one-half times as long as distance between rows of bristles, more closely spaced within each row.

Male.—Similar to female except 2.7 times as long as wide; frons as in male of *inimicus*; interstitial punctures on disc as large as those of striae, very feebly granulate; stria punctures smaller on disc and declivity, somewhat obscure on declivity; vestiture with interstitial setae on disc rather narrowly scalelike, truncate, those on declivity longer, more slender and almost pointed at their apices.

Type Locality.—Zamorano, Morazan, Honduras.

Type Material.—The female holotype, male allotype, and 16 paratypes were collected at the type locality on April 18, 1964, 700 m., No. 506, by S. L. Wood, from branches of *Celtis iguanaea*; 14 paratypes bear identical data except they are lot No. 534, from *Calliandra houstoniana*.

The holotype, allotype, and paratypes are in my collection.

Hylocurus alternus, n. sp.

The only species known to me that is closely related to this one is *inaequalis* Wood; however, it has the male declivital spines much less highly developed. The development of declivital spines is similar in magnitude to *medius* Wood, but the relationship to the latter species is remote. Females of this species lack the abundant frontal vestiture of *inaequalis*.

Male.—Length 2.5 mm. (paratypes 1.7-2.5 mm.), 2.5 times as long as wide; color very dark brown, almost black.

Frons concealed in type. In male paratype, convex and granulate above, transversely impressed and punctured below a transverse carina formed at upper level of eyes by four basally confluent tubercles; vestiture inconspicuous.

Pronotum 1.1 times as long as wide; widest near base, the sides feebly arcuate and converging very slightly on basal two-thirds then rather broadly rounded in front; anterior margin armed by about 12 coarse serrations; summit in front of middle; posterior area subshining, rather finely punctured, the posterior margin of each puncture subasperate, more coarsely sculptured toward summit. Vestiture consisting of short, inconspicuous hair.

Elytra 1.4 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel to declivital base; profile of posterior margin interrupted by projection of spines on interspaces 9 and 3 and by sutural apex; striae not impressed, the punctures large, deeply impressed; interstriae narrower than striae, irregularly, sparsely punctured, each ending posteriorly at declivital margin in a tubercle or spine. Declivity abrupt, very steep; upper and lateral margins armed by a row of tubercles, those on interspaces 2, 4 and 6 distinctly shorter, all tubercles abruptly declivous behind, 9 longer and projecting; declivital face convex, coarsely punctured with two rather coarse tubercles on interspace 3 and about four smaller ones on middle third of 1; apex narrowly acuminate. Vestiture consisting of short, stout, bristles.

Female.—Similar to male except frontal carina absent, the frons more finely sculptured; anterior margin of pronotum finely serrate; elytra not abruptly declivous, without a marginal row of tubercles on declivity; each interspace bearing about three to five small tubercles on upper or lateral half of declivity.

Type Locality.—twenty-one km. south-east of Liberia, Guanacaste Prov., Costa Rica.

Type Material.—The male holotype, female allotype, and 39 paratypes were collected at the type locality on July 10, 1966, at an elevation of

about 50 m., from a branch of an unidentified tree, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Hylocurus aberrans, n. sp.

This species is not allied to any other representative of the genus known to me. The sutures of the antennal club are more strongly procurved than in other *Hylocurus*, but less so than in *Micracis*. The posterior face of the anterior tibia is tuberculate as in *Hylocurus*; the posterior extremity of declivital interspace 9 almost reaches the costal margin thereby resembling somewhat certain species of *Micracis*.

Male.—Length 2.2 mm., 2.6 times as long as wide; color dark reddish brown.

Frons broadly convex with a slight transverse impression just above epistomal margin; surface finely, regularly granulate. Antennal club with two procurved sutures, 1 extending two-fifths from base, 2 extending four-fifths from base.

Pronotum 1.2 times as long as wide; widest on basal half, the sides feebly arcuate, rather broadly rounded in front; anterior margin armed by 16 or more serrations; summit in front of middle; posterior area reticulate, with small, subgranulate punctures of moderate abundance. Vestiture consisting of short, erect scales with a few bristles in asperate area.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel to base of declivity then slightly wider at middle of declivity; posterior outline interrupted by declivital spines on interspaces 7, 8, and 9 and by short, broad, sutural apex; striae slightly impressed, the punctures deep, coarse, much smaller toward base; interstriae about half as wide as striae, the punctures on 1 moderately large, others mostly minute. Declivity abrupt, very steep, almost entirely margined by a row of tubercles or spines; tubercles at base of declivity on interspaces 1 and 2 not pointed, abruptly declivous behind, those on 2 to 8 produced into increasingly large and pointed toothlike spines, 9 similar but lower and extending nearer elytral apex than normal for this genus; apex not strongly produced, its margin subserrate, the small dentitions about half as high as apex of elevation on interspace 9; central area coarsely punctured, interspace 3 slightly elevated near center and bearing three small teeth, 1 on lower third gradually elevated to apex and finely serrate. Vestiture consisting of a few stout bristles or scales at margin and on interspaces 1 and 3.

Female.—Similar to male except frons less strongly convex, finely punctured, ornamented by stout, short, rather sparse, setae; scape flattened and bearing a tuft of long, coarse setae; anterior margin of pronotum almost unarmed; elytra more finely sculptured, the declivity convex, without marginal ring of tubercles, the striae regularly punctured, odd numbered interspaces bearing several rounded granules; rows of broad scales on upper half of all declivital interspaces.

Type Locality.—Dominical, Puntarenas Prov., Costa Rica.

Type Material.—The male holotype and female allotype were taken from the same tunnel at the type locality on December 9, 1963, at sea

level, by S. L. Wood, from a small branch of a recently cut unidentified tree.

The holotype and allotype are in my collection.

Hylocurus incomptus, n. sp.

Fig. 3



Fig. 3. *Hylocurus incomptus* dorsolateral aspect of male elytral declivity.

This species is allied to *femineus* Wood, but it is readily distinguished by absence of sexual dimorphism on the frons, by the much more finely sculptured elytral disc and declivity, and by the steeper elytral declivity.

Male.—Length 2.3 mm. (paratypes 1.9-2.5 mm.), 2.6 times as long as wide; color black.

Frons moderately convex, the epistomal margin slightly elevated; a conspicuous, transverse carina occupying median half at upper level of eyes; surface coarsely reticulate, the sparse punctures minute; vestiture inconspicuous except on epistomal margin. Eye smaller than related species.

Pronotum 1.2 times as long as wide; widest at base, sides almost straight, converging anteriorly slightly on posterior two-thirds, broadly rounded in front; anterior margin subserrate; sculpture as in *femineus* with tubercles behind summit finer, becoming obsolete at base; vestiture inconspicuous, hairlike.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel on basal two-thirds, rather abruptly rounded behind, median fourth extending into a rather well-developed mucro; striae not impressed, the punctures fine, shallow but distinct; interstriae about three times as wide as striae, marked by irregular lines, almost flat, the punctures minute, widely separated, becoming finely granulate on posterior fourth. Declivity convex, very steep; striae punctures obscure; interstriae 3 weakly, 9 moderately elevated, 1 feebly raised and terminating apically in mucro; all interstriae with a row of tubercles on upper third, minute on 2, rather coarse on 3 and last tubercle on 9, those on 3 extend to middle, on 1 two or three minute granules scattered on lower half. Vestiture hairlike, consisting of rows of short striae, and slightly longer interstitial setae on declivity.

Female.—Similar to male except evidently very slightly more finely sculptured; declivital vestiture longer and more abundant.

Type Locality.—Volcan de Agua, Esquintla, Guatemala.

Type Material.—The male holotype, female allotype, and 63 paratypes were collected at the

type locality on May 19, 1964, 1,000 m., No. 616, by S. L. Wood, from an old fallen limb about 20 cm. in diameter. It appeared that two or more generations had been completed in the same piece of wood.

The holotype, allotype, and paratypes are in my collection.

Hylocurus microcornis, n. sp.

This species evidently is allied to *cancellatus* Blandford, but it differs in the female frons, in the absence of a tubercle on the male declivital interstriae 5, and evidently in the very small antennal club.

Male.—Length 2.7 mm. (paratypes: male 2.7-3.0, females 2.9-3.0 mm.), 2.7 times as long as wide; color black.

Frons weakly convex, ascending slightly toward epistoma; surface very closely, subgranulately punctured, with a transverse carina occupying median third at level immediately below upper level of eye. Antennal club very slightly longer than distance equal to width of eye, 1.7 times as long as wide.

Pronotum 1.06 times as long as wide; widest on basal third, the sides weakly arcuate and converging slightly to anterior third, then rather narrowly rounded in front; anterior margin armed by eight teeth; anterior slope asperate, posterior area closely tuberculate, the interstriae rather coarsely reticulate; vestiture inconspicuous, hairlike.

Elytra 1.9 times as long as wide, 2.0 times as long as pronotum; striae slightly impressed on posterior third, the punctures deep, small at base, increasing in size toward declivity; interstriae as wide as striae, weakly convex except near declivity, terminating abruptly at margin of declivity in a blunt, nonprojecting spine, the punctures rather fine, uniseriate. Declivity abrupt, somewhat convex within ring of subequal marginal tubercles (except those on 1 smaller); costal margin near apex subserrate; striae punctures impressed, in rows; interstriae shining, 1 bearing nine small pointed tubercles, 3 with three small granules, lateral interstriae unarmed, mucro well developed, reticulate. Vestiture confined to declivity, consisting of minute striae hair and rather long, slender bristles.

Female.—Similar to male except frons above more nearly flattened, below slightly more protuberant, ornamented on median two-thirds by a conspicuous tuft of rather long, yellow hair from near epistoma to vertex, median area immediately above epistoma smooth and shining, remaining area rather finely reticulate-granulate, punctures obscure, carina absent; anterior margin of pronotum unarmed; tubercles on declivital margin absent; declivital striae on disc, interstriae except 2 armed by fine tubercles, those on 1, 3, 7 and 9 extending to middle of declivity, others ending on upper fourth; elytral vestiture finer, shorter, extending to disc.

Type Locality.—Twenty-six km. east of Texmelucan, Puebla, Mexico.

Host.—*Salix* sp.

Type Material.—The male holotype, female allotype, and 6 paratypes were collected at the type locality on June 13, 1967, 2,900 m., No. 29, by S. L. Wood, from branches of willow.

The holotype, allotype, and paratypes are in my collection.

*Phloeocleptus plagiatu*s, n. sp.

This species is closely allied to *obscurus* Wood, but may be distinguished by the much larger size, by the transverse impression of the lower frons and presence of a low median elevation above, by the absence of teeth on the anterior margin of the male pronotum, and by the somewhat more strongly elevated declivital interstriae 9.

Male.—Length 1.5 mm. (paratypes 1.4-1.8 mm.), 1.4 times as long as wide; color very dark brown, almost black in mature specimens.

Frons convex above, a moderate, transverse impression at level of antennal insertion; a short, longitudinal, median carina at upper level of eyes; surface smooth and shining at center below, becoming coarsely reticulate elsewhere, finely punctured toward smooth area, a few fine granules laterally and above; vestiture inconspicuous except near epistoma. Antennal scape short, about two and one-half times as long as wide, bearing a small tuft of hair; club small, two straight sutures indicated by setae only at lateral margins.

Pronotum 1.0 times as long as wide; sides almost straight on posterior half, converging to a feeble constriction just anterior to middle, rather broadly rounded on the unarmed anterior margin; anterior slope asperate to summit, summit at middle; posterior area rather coarsely reticulate, with small, isolated granules decreasing in abundance toward basal margin, granules replaced by minute punctures in lateral areas. Vestiture moderately abundant, consisting of stout hairlike setae, longer in median area behind summit.

Elytra 1.4 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, subacutely mucronate behind; striae feebly if at all impressed, the punctures of moderate size and depth; interstriae shining, as wide as striae, the punctures fine, uniseriate. Declivity convex, steep; striae punctures reduced, obscured by subgranulate reticulation of entire declivital surface; interstriae each armed on upper half by a series of small tubercles, 1 and 3 feebly elevated, 9 more strongly raised and subcarinate on basal half; apex gradually extended toward poorly developed mucro. Vestiture on disc and declivity consisting of fine, erect striae hair, and slightly longer, moderately stout interstriae bristles; more conspicuous on declivity.

Female.—Similar to male except antennal scape triangular and bearing a larger tuft of hair; elytral vestiture finer and somewhat shorter.

Type Locality.—Seven km. west of Tepic, Nayarit, Mexico.

Type Material.—The male holotype, female allotype, and 33 paratypes were collected at the type locality on July 13, 1965, about 1,000 m., No. 240, by S. L. Wood, from cut branches of a roadside shade tree. The tunnels were in the phloem and were similar to those of *caudatus* Wood.

The holotype, allotype, and paratypes are in my collection.

Phloeocleptus nanulus, n. sp.

This species is allied to *plagiatus* Wood, described above, but it is easily distinguished

by the uniformly convex frons, by the armed anterior margin of the pronotum in both sexes, by the interstitial granules on the male disc, by the greater development of tubercles at the base of the elytral declivity and by the more strongly elevated interstriae 9.

Male.—Length 1.5 mm. (paratype 1.6 mm.) about 2.5 times as long as wide; color almost black.

Frons convex except epistomal margin weakly elevated; surface subreticulate, with small isolated granules except almost smooth in median epistomal area; vestiture inconspicuous. Antennal scape short, about twice as long as wide, bearing a small tuft of hair.

Pronotum 1.0 times as long as wide; outline as in *plagiatus* but anterior margin armed by four teeth, the median pair larger; sculpture as in *plagiatus*, vestiture coarser.

Elytra about 1.6 times as long as wide (elytra spread slightly), 1.6 times as long as pronotum; outline as in *plagiatus*; striae perhaps feebly impressed, the punctures rather small, deep, larger posteriorly; interstriae almost as wide as striae, the punctures finely granulate (sub-vulcanate), the granules slightly larger near declivity. Declivity steep, convex; as in *plagiatus* except all tubercles slightly larger particularly those at base of declivity in lateral areas; interstriae 9 much more strongly elevated. Interstitial bristles on declivity longer and coarser than in *plagiatus*.

Female.—Similar to male except antennal scape longer, wider, and bearing a larger tuft of hair; anterior margin of pronotum armed by two small teeth; discal interstriae not granulate; lateral declivital tubercles smaller, interstriae 9 not as strongly elevated; declivital vestiture not as coarse.

Type Locality.—Seven km. west of Tepic, Nayarit, Mexico.

Type Material.—The male holotype, female allotype, and one female paratype were collected at the type locality on June 13, 1965, about 1,000 m., No. 240, by S. L. Wood, in series with *plagiatus* which was described above.

The holotype, allotype, and paratype are in my collection.

Phloeocleptus parvus, n. sp.

This species is more closely allied to *plagiatus*, described above, than to others in the genus, but it is easily distinguished by the more slender antennal scape, by the presence of several rather large punctures on the base of the pronotum, and by the reduced number of tubercles on the elytral declivity.

Male.—Length 1.3 mm., 2.6 times as long as wide; color dark brown (probably not fully mature).

Frons not visible. Scape little if any wider than pedicel, about three times as long as wide.

Pronotum 1.16 times as long as wide; widest behind middle, sides feebly arcuate, almost straight and parallel on basal two-thirds, broadly rounded in front; anterior margin unarmed; summit in front of middle; posterior area reticulate, a few small, isolated granules near summit, several moderately large, deep punctures toward basal margin and in entire lateral area; vestiture fine, largely abraded.

Elytra 1.5 times as long as wide, 1.3 times as long as pronotum; outline and disc as in *plagiatus*. Declivity steep, convex, shining to apex; striae punctures slightly confused; interstriae 1 and 2 unarmed, 2 greatly narrowed near middle, 3 armed by a tubercle at middle and another at junction with 7, 7 also bearing a small tubercle at declivital base, 9 more strongly elevated than in *plagiatus*. Vestiture confined to declivity, consisting of very short striae and moderately long, stout, interstitial bristles.

Type Locality.—Los Corchos, Nayarit, Mexico.

Type Material.—The male holotype was collected 2 km. south of highway 15 on the Los Corchos road on July 10, 1965, No. 206, by S. L. Wood, from a broken branch of an unidentified tree.

The holotype is in my collection.

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**Brigham Young University
Science Bulletin**

**A STUDY OF THE
WEEVIL TRIBE CELEUTHETINI
OF THE SOLOMON ISLANDS
(COLEOPTERA: CURCULIONIDAE)**

by

VASCO M. TANNER



BIOLOGICAL SERIES — VOLUME X, NUMBER 3

JUNE, 1969

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BIOLOGICAL SERIES

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(Lord Howe Is)

Kela I

Levanua I

PACIFIC OCEAN

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SANTA ISABEL ISLAND

St George I

MALAITA ISLAND

GUADALCANAL ISLAND

SAN CRISTOBAL ISLAND

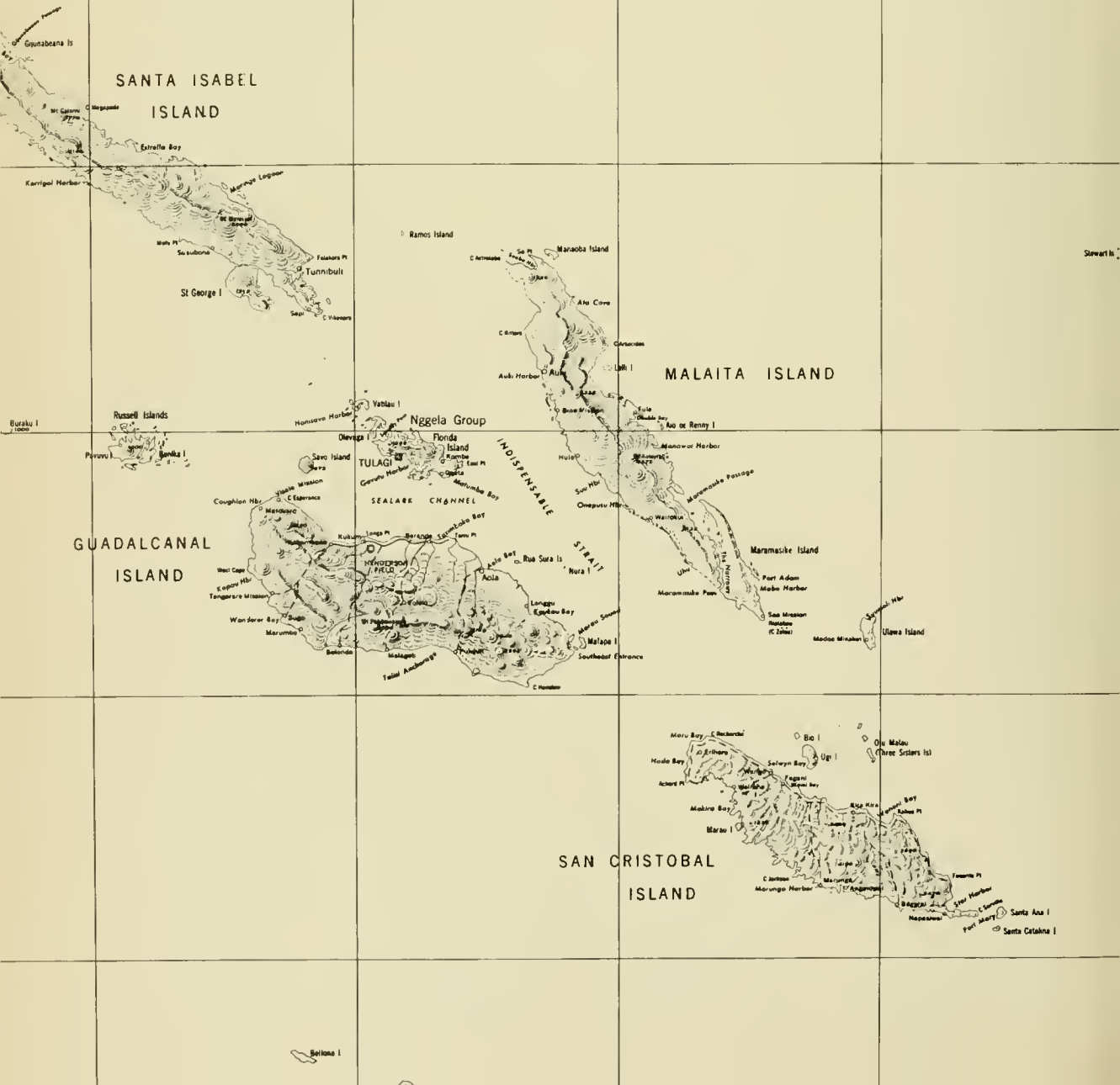




Fig. 1. Map of the Solomon Islands. By permission of the United States Army Map Service.

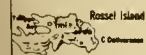


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A STUDY OF THE WEEVIL TRIBE CELEUTHETINI
OF THE SOLOMON ISLANDS
(COLEOPTERA: CURCULIONIDAE)

by

Vasco M. Tanner¹

INTRODUCTION

This study is concerned with the genera and species of the tribe Celeuthetini known to occur in the Solomon Islands. The tribe is confined, in the main, to New Guinea and neighboring Islands. With the exception of *Celeuthetes*, the genera and species of Celeuthetini on which this paper is based are endemic to the Solomon Islands. On the basis of collections, *Celeuthetes*, has a wide distribution from Australia to the Moluccas.

The Solomon Islands consist of eleven large islands which form two chains. The northern row of islands are Buka and Bougainville, just south of New Britain, followed by Choiseul, Santa Isabel, and Malaita. The southern group, which essentially parallels the northern row, consists of Vella Lavella, Kolombangara, New Georgia, Russell, Guadalcanal, and San Cristobal.

Bougainville, the largest of the Solomon Islands, has an area of 3,900 square miles, while Guadalcanal, the second largest, is 2,500 square miles in area. The main topographical features of the islands are the 10,000-foot active volcano, Mount Bally, on Bougainville and an 8,000-foot peak on Guadalcanal (map, Fig. 1). The climate is tropical; the average temperature is about 82 degrees Fahrenheit. During the rainy season, from January to March, the temperature and humidity are high. The weather from April to November is fairly cool. In general the climate, flora, and fauna of the Solomon Islands are similar to that of Guadalcanal. The topography, direction of the mountain ranges, and size of the islands have influenced the floral patterns, density of the plant growth, and, to some extent, determined the insect life on each of the islands (Gressitt 1961). The following observations made on the climate and plant life of Guadalcanal may be applicable to the other islands of the Solomon group.

Mr. Robert C. Pendleton, who spent twenty-two months on the Solomon Islands in 1944-45, published his findings on "The Rain Shadow Effect on the Plant Formations of Guadalcanal" (1949). The following excerpts are from this study.

Guadalcanal is well within the true tropic belt and the work of many plant geographers indicates that a rain forest type of vegetation should be expected. However, this island differs in having the major portion of the North Coast covered with coarse grass while a true rain forest vegetation occurs in the south portion and on the mountains.

The main mountain ranges on the island are approximately parallel and occupy a central position. Comprehensive ground studies were made only on the north coastal plain, because travel to other portions was extremely difficult. Guadalcanal is the only island of the group having a mountain chain at right angles to the prevailing wind direction. It is characterized by having a rain forest on the south side and grasslands on the north side of the island. The ecological factors responsible for the grasslands of the island are both climatic and topographic. In the rain shadow insufficient rain falls during several months to support a forest.

This great ecological diversity which prevails in the Solomon Islands, no doubt, accounts for the many species of insects found on the Islands.

Although knowledge of the Celeuthetini has been accumulating since the pioneer contributions of Guérin-Meneville (1841); Wallace (1854-1862); Lacordaire (1861); Pasco (1885); Cheveolat (1885); Faust (1897); Heller (1910, 1934); Gunther (1937); E. C. Zimmerman (1942); and J. L. Gressitt (1966 a & b); the rich insect fauna of the Solomon Islands is still poorly known.

Collecting throughout the year on all areas of the islands will, no doubt, produce many ad-

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ditions to the fauna as well as contribute information concerning the economic importance and life history of the insects. The specimens that have come under my observation have been collected mainly at a few coastal centers on the Solomon Islands.

The monumental study by Sir Guy Marshall (1956) brought order out of a previously disorganized classification of the Celeuthetini. It represents a critical enlargement of the revisional work of Faust (1897). Faust had recognized 31 genera as belonging to the tribe but had failed to discern the generic characters and groupings of the tribe. Marshall pointed out the restricted

range and high endemicity of several of the genera as evidenced by the separation of the 36 species of the old wide-spread genus *Trigonops*. These he considered as confined to the Solomon Islands area.

Several species known to occur on the islands have not been described, since they are represented in collections only by a single specimen. The type material of all new species described in this study have been deposited in the collections from which the specimens came to me by loan. Type specimens are designated and their disposition indicated as a part of each description.

SYSTEMATIC CONSIDERATIONS

The subfamily Otiorrhynchinae,² the broad-nose weevils, as now constituted, is separated into 15 tribes, genera and species many of which are world-wide in their distribution. The tribe Celeuthetini, however, is restricted to the Pacific area, extending from Northern Australia, westward to Java, northward from the Celebes to the Philippine Islands, southeastward to Halmahera, Admiralty, Bismarck, New Britain, New Ireland, Solomon, and New Hebrides Islands. The Philippines and New Guinea seem to be the two focal areas of the tribe since of the 72 known genera 23 are endemic to New Guinea, 10 to the Philippines, and 5 to the Solomon Islands.

The important tribal characteristics of Celeuthetini are rostrum as long or longer than head, robust, bent downward at apex, narrowed in the middle; scrobes angular, well developed, antennae long, scape extending to the anterior portion of the prothorax, funicular club elongate; transverse sulcus separating rostrum from head; clytra not wider than prothorax at base, with shoulders rounded or rectangular; mesepimera much reduced, remote from the base of the elytra; metepisternal suture much abbreviated front coxae more or less separated, except in some very small species; corbels of the hind tibiae placed in a more dorsal position, so that the tarsal cavity is largely, or even entirely concealed when the tibia is viewed on its inner

surface, level of the corbel with its inner edge entirely bare of setae.

The keys to the genera and species are based upon the morphological characters as revealed by careful study of specimen of each species. Since R. M. Heller described many of the species included in this study, it was necessary that specimens from the type series be made available. Through the kindness of Dr. Gotz cotype specimens of all of Heller's species were loaned to me and proved to be invaluable for making comparisons and drawings. As a result specimens of 43 of the species have been studied, 23 of which were designated as *Typus* specimens. A *Typus* (sic) specimen of the distinctive species *Atactophysis cordata* Hllr., rare in collections and unknown to Sir Guy Marshall, was made available to me. The *Typus* specimen is labeled Solomo Ins. T. Bodecker. No other specimens have been observed. A drawing of the *Typus* specimen is included in this study.

Great care has been taken to have the drawings represent the correct proportions of the insect structures as well as the vesture. A drawing of the insect in toto illustrating the rostral shape and sculpturing, along with that of the eyes, antennae, prothorax, and elytra will supplement and clarify the accompanying descriptions. A description is a subjective appraisal of the objective material on the part of the author, which is oft-times brief and minus important at-

²Recently it has been proposed, because of priority, that this subfamily be known as Brachyrhynchinae. See *Coleopterorum Catalogus* pars 160, 290-315 for a listing of the tribes.

tributes of the object. A good drawing, therefore, is more objective and thus is an important supplement to an insect description.

Similarity of genitalia was noted after many species had been studied. Therefore, illustrations of female and male genitalia of only *Trigonops becki* and *T. platessa* are provided as representative of the species of this genus. A widely debated subject today among entomologists is that of species classification. In order to justify the efforts put forth in this study I wish to present the following point of view as it relates to the procedures and proposals of this study. Systematic workers acquainted with the theory and practice of present-day systematic zoology will admit that to continue to describe new species, as some have done in the past, is only to add to the great number of partially known "species" with which taxonomic literature is encumbered. The solution, however, would seem not to go to the extreme and abandon the "species level" activity as suggested by Oldroyd, (1966). Man's knowledge of the animate world is largely due to the results of past practices of segregating, describing, and naming of species. As a result much progress has been made in the categorization of plants and animals. It is granted that some past species taxonomy is inadequate since it is based upon a meager description of a single type-specimen. Presently the refinement of naming a new species is based upon an analysis of a number of specimens, as to internal as well as external morphology, along with data on habitat, life history, distribution, and food habits. A description based upon the above, and accompanied by drawings, conveys information on an objective basis. It makes possible the recording of minute details, which are free from those difficulties which are present in the verbal description. This has been the attempted approach in dealing with the species of this study.

The Celeuthetini are restricted to the oceanic Pacific Islands, as pointed out above, and since so little is known about the insect fauna of the New Guinea-Solomon Islands area (Gressitt, 1961), studies following Marshall (1956), should aid in pointing up the endemism and distribution of this tribe.

A study of the origin of the insect fauna of the Solomon Islands presents many interesting and difficult problems. The origin of the fauna is closely associated with the origin of the islands. Recently much interest has been manifest in the different theories of continental drift. Darlington (1965) is of the opinion "that the southern continents have drifted." Additional research, how-

ever, must be carried on before the picture of the past relationship of the Solomon Islands with the surrounding island complex is clarified. Along with additional knowledge as to the age and origin of the islands must be added information dealing with the geology, geography, climate, ecology, and a more complete sampling of the islands insect fauna. More intensive collecting, especially in the interior of the larger islands, will, no doubt, extend the range of presently known species, as well as result in the discovery of many new ones. As an example we may cite Gressitt's (1966) paper dealing with the Papuan weevil genus *Gymnopholus* (Leplopiinae) which points up the possibilities of intensive collecting on the mountainous areas of the islands. Prior to Gressitt's study only 14 species were consigned to *Gymnopholus*. Collecting at high altitudes on the northeast interior of New Guinea resulted in his adding 32 new species to the genus.

The faunal relationships of insects, amphibians and reptiles of the Solomon Islands and of New Guinea suggest that at an early geological period these islands were connected. It has also been pointed out by Marshall (1956) and students of the reptiles that there is a faunal relationship among species found in the Solomons, the northern islands, and Asian mainland. The accumulated information on the origin and phylogeny of the fauna of these oceanic islands indicates that it is predominately Oriental.

The following recent report on the "Paleogeography of the Tropical Pacific" by Menard and Hamilton (1961) supports the belief that many of the islands are oceanic:

The oldest known fossil fauna from the Pacific Basin is the Middle Cretaceous reef coral-rudistid fauna from the flat tops of seamounts in the Mid-Pacific Mountains. A number of other localities have been dated as early and late Eocene. There are enough of these dates to indicate that the present topography or ridge, seamounts, and islands probably originated during and after the Cretaceous. The evidence indicates that there were never any sunken continents in the area, but the ideas concerning animal migration by island stepping-stones (between present and former islands) appear to be more and more valid.

The fact that many of the islands are continental while others are oceanic, that some are geologically much older, also, that some have been separated or isolated and surrounded by deep water for longer periods of time, and that climatic and ecological conditions are different on many of the islands, present conditions that

have influenced the rate of evolution, survival, and dispersal of the species of the respective islands. Too little is now known about the rich insect fauna of the Solomon Islands. In this paper 25 species of *Trigonops* are discussed, and of this number 7 are known to occur on Bougainville, and 6 are known from Guadalcanal.

This study has revealed that much more collecting and association of the specimens with

their host plants along with the gathering of ecological information is necessary before conclusions as to the extent of the fauna and its economic importance will be available. A program of this nature will necessitate segregation of the specimens into groups or species and the designation by some symbol or name of each group if we are to deal intelligently with the specimens of this tribe.

ACKNOWLEDGMENT

This study was possible only because of the suggestions, cooperation, and specimen material made available by the late Sir Guy Marshall of the British Museum of Natural History, Herrn Dr. Wilhelm Gotz of the Dresden Museum, and Dr. J. L. Gressitt of the Bishop Museum, Honolulu. Marshall made available specimens of *Trigonops* from the British Museum collection and also determined and made comments on 21 species belonging to the tribe Celeuthetini which I sent to him from the Brigham Young University Collection. My association with him at the British Museum in 1957 was most rewarding. I also wish to thank E. China, R. T. Thompson, and J.P. Doncaster, personnel of the British Museum, who have been patient with the return of museum specimens. Dr. Gotz loaned cotypes of species of *Trigonops*, *Kietana*, *Atactophysis*, *Colposternum* and *Hoplotrigonops* described by Dr. K. M. Keller, and cotypes of four species of *Platyacus* described by J. Faust. I am grateful to these entomologists and staff members for their aid rendered in this project.

I also extend my thanks to J. L. Gressitt, Chairman of the Entomological Staff, Bishop Museum, for a loan of specimens which he collected in the Solomon Islands. Thanks is also due Mr. Hugh B. Leech, Curator of Insects, California Academy of Sciences, San Francisco, and Mrs. Rose Ella Spilman, U. S. National Museum for a loan of specimens of the genus *Trigonops*.

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To the late Dr. D Elden Beck, Professor Ernest Reimschuessel, the late Harry P. Chandler, and Dorald Taylor, who were stationed on Guadalcanal and Morotai Islands in 1944 and 1945, as personnel of the United States armed forces, I express my appreciation and thanks for the results of their collecting efforts. They sent to the Brigham Young University, their alma mater, thousands of insect specimens.

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KEY TO THE GENERA OF CELEUTHETINI FOUND ON THE SOLOMON ISLANDS

1. (2) Rostrum abruptly declivious dorsally at the apex.
2. (3) Elytra often granulate but without conical tubercles.
3. (4) Tibiae not carinate dorsally.
4. (22) Elytra with more than ten striae, sometimes confused.
5. (7) Rostrum with the basal sulcus broadly interrupted in the middle the rostrum being there continuous with the frons.
6. (5) Head constricted behind the eyes; mentum sessile, prothorax granulate; elytra indistinctly striate, rather densely granulate (Bougainville Is.) *Zeugorrhinus* Marshall
7. (8) Rostrum with the basal sulcus not interrupted.
8. (9) Front tibiae not denticulate.
9. (10) Joint 2 of the funicle, not or but slightly longer than 1.
10. (16) Meosternal process longer than the shortest distance between the coxae.
11. (12) Rostrum dilated apically.
12. (13) Funicle stout, widest at the base narrowing distally; eyes nearly flat, not projecting beyond the temples, mentum with only two setae; stria 12 on the elytra abbreviated; front coxae in the middle of the prosternum (Solomon. Isl.) *Kietana* Heller
13. (12) Funicle slender, not narrowing distally; eyes convex, projecting.
14. (15) Mentum with four or more setae; front coxae in the middle of the prosternum; stria 12 abbreviated.
15. (16) Rostrum with the dorsal area shallowly excised, the narrowest part two to three times as wide as the apex of the scape, the declivity without scales or a dorsal elevation (New Guinea, Solomon Islands) *Celeuthetes* Schonh
16. (10) Mesosternal process as broad as long or broader than long.
17. (18) Front coxae nearer to the front margin of the prosternum; metasternum shorter than a median coxa.
18. (21) Rostrum with the basal sulcus not produced downward in front of the eyes.
19. (20) Prothorax with the basal margin elevated; elytra cordate flattened; metasternum with the deep rugose depression on each side. (Solomon Isl.) *Atactophysis* Heller
20. (19) Prothorax with the base not elevated; elytra ovate, convex, metasternum without depressions.
21. (18) Rostrum with the basal sulcus produced downward in front of the eyes.
22. (4) Elytra with ten regular striae, but the tenth often abbreviated.
23. (28) All of the femora with one or more small teeth; mesosternal process transverse.
24. (25) Front margin of prosternum sinuate; rostrum distinctly longer than broad; frons very steep, nearly vertical. its width less than the length of an eye.

eyes directed obliquely forward; with only four visible ventrites. (Solomon Isl.) *Platyacus* Faust

25. (23) Femora without teeth.

26. (27) Mesosternal process much broader than long.

27. (28) Declivity rostrum squamose.

28. (29) Funicle with joint 2 not longer than 1.

29. (33) Eyes more or less conical, highest behind the middle mostly very strongly produced. Elytra with stria 10 approaching very closely to 9, the punctures comparatively larger in the basal, third, much smaller behind; five visible ventrites, ventrites 3 and 4 narrow in width (Solomons) *Trigonops* Guerin

GENUS ZEUGORRHINUS MSHL. (1956)

Marshall, The Otiorrhynchine Curculionidae of the tribe Celeuthetini (Col.), 1956, p. 28, British Museum, London

Fig. 2

Marshall based the genus *Zeugorrhinus* on a species collected at Kieta, Bougainville Islands, in 1937 (J. L. Fraggott). As far as the writer is aware, *granulatus* is the only species now assigned to the genus. No specimens of this species have been available for study. Marshall indicates that this taxon is most nearly allied to *Elythrocheilus* Fst., consisting of some 20 species which are mainly found on New Guinea, Louisiade Archipelago and Woodlark Islands. An examination of several specimens of *Elythrocheilus confinis* Fst. from Oro Bay, New Guinea collected by Harry P. Chandler, 1944, confirms Marshall's statement as to the characteristics of the genus *Elythrocheilus*; "the basal sulcus of the rostrum is complete; the head is not constricted behind the eyes; the prothorax is vertically truncate at the apex; the elytra are strongly carinate at the base; and the mesosternal process is somewhat transverse and almost parallel-sided." *Zeugorrhinus* is characterized as follows: "the head constricted behind the eyes, separated from the rostrum by a deep sulcus which is rather broadly interrupted in the middle but is continuous downward laterally at apex, the basal margin finely carinate. Mesothoracic process narrowly triangular much longer than broad."

A good illustration of *Z. granulatus* Mshl. contained in Marshall's paper is here reproduced for the convenience of those interested in the Celeuthetini of the Solomon Islands.

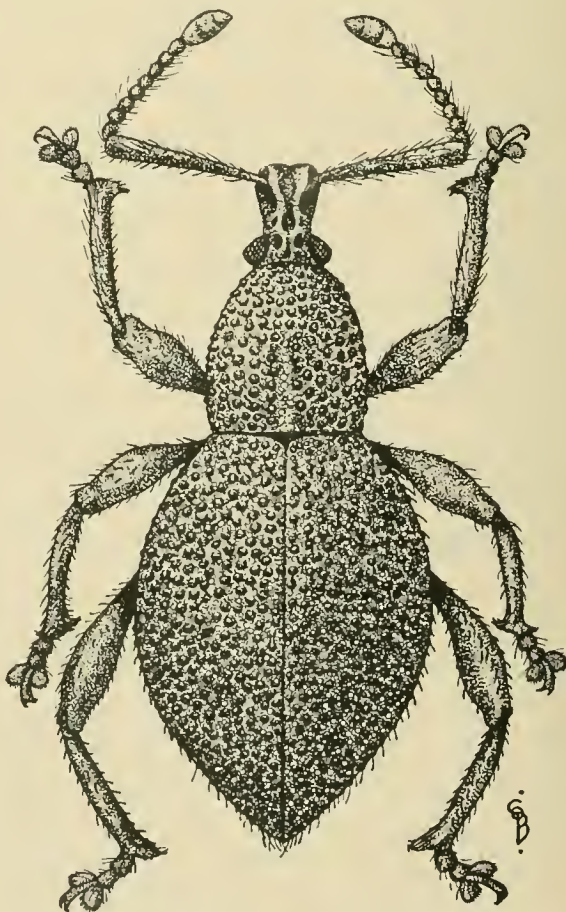


Fig. 2. *Zeugorrhinus granulatus* Mshl. - ♀

GENUS KIETANA HELLER (1910)

Heller, Wien. Ent. Zeit., XXIX, 1910, p. 195
 Marshall, The tribe Celeuthetini, 1956, p. 38

This genus may be characterized as follows:

Head level with rostrum, separated from it by a deep curved sulcus; rostrum longer than broad, dilated at genae, apical declivity devoid of scales, dorsum with two carinae and an eleva-

tion at the top of declivity. Antennae scape stout, rugosely punctuate and parallel sides; funicle stout at base and narrowing distally, joints I and 2 equal. *Prothorax* about as long as broad, granulate, not constricted at apex. *Elytra* broadly ovate, with 12 striae, twelfth abbreviated. *Legs*, with femora moderately clavate, hind pair not reaching apex of elytra. Prosternum with coxae in middle and contiguous; ventrite 2 longer than 3 and 4, 1 and 2 granulated laterally.

Key to Species of KIETANA HELLER

Marshall, 1956, p. 38

1. (7) Funicle with joints 4-6 transverse or not longer than broad.
2. (3) Setae on the elytra and declivity spatulate and recumbent; prothorax with kidney-shaped granules (Bougainville Is.) size 9.8 mm in length—4 mm in breadth. Fig. 3 *episomoides* Hllr.
3. (2) Setae on declivity of the elytra not spatulate, longer, stouter erect or suberect.
4. (5) Prothorax without punctures, the granules dense and simply convex; elytra with the indistinct granules in the striae of about the same size as those on the intervals (Russel Is.) size 5.5–8.0 mm., in length—2.5–4.0 mm in breadth *tessellata* Mshl.
5. (4) Prothorax long, feebly rounded laterally, disc flat longitudinally, granules lunate due to a lateral puncture from which a small brown setae issues, granules in the striae about the same size as those on the intervals. (Gua-dalcanal Is.) size 8.9–9.1 mm., in length—4.0 mm in breadth. Fig. 4 *gressitti* n. sp.
6. (5) Prothorax distinctly rounded laterally, disc elevated near base slopping toward the apex; discal granules large, lunate owing to a large puncture on the inner side of each; granules in the striae much smaller than those on the intervals (Isabel Is.) size 8.0 mm in length—3.8 mm in breadth *isabellae* Mshl.
7. (1) Funicle with all joints distinctly longer than broad; discal granules on pronotum lunate; setae on the elytra subrecumbent (Shortland Is.) size 8–10 mm in length—3.7–4.8 mm in breadth *aluensis* Mshl.

Kietana episomoides Heller
 Wien. Ent. Zeit. 39: 195, 1910.

Fig. 3

The following description was made from one cotype specimen kindly loaned by Dr. Wilhelm Gotz of the Dresden Museum.

Derm black, with white scales; pronotum with narrow median stripe of denser scales; elytra with scales grouped between large granules on intervals. *Head* slightly punctuate up to vertex, frons convex, eyes obovate, slightly convex. *Rostrum* stout and not so roughly punctuate as in some other species of *Kietana*; lateral and angular area with long white setae. *Antennae* scape

parallel-sided, widening slightly from base to apex; funicle joints 1-2-3-7 equal in length; joints 4-5-6 smaller and equal, with long brown setae. *Prothorax* slightly longer than broad, gently rounded, laterally, widest at middle; dorsum feebly convex longitudinally, granules on disc lunate due to a puncture on the inner side of each one; each bearing a spatulate recumbent white seta. *Elytra* ovate, longer than broad, widest at apical third, declivity abrupt, with long flat setae, disc flat with large granules irregularly placed along intervals making wavy arrangement, seta issuing from side of granule, small granules along stria, and with scales between shining granules. *Legs*, femora and tibia red-

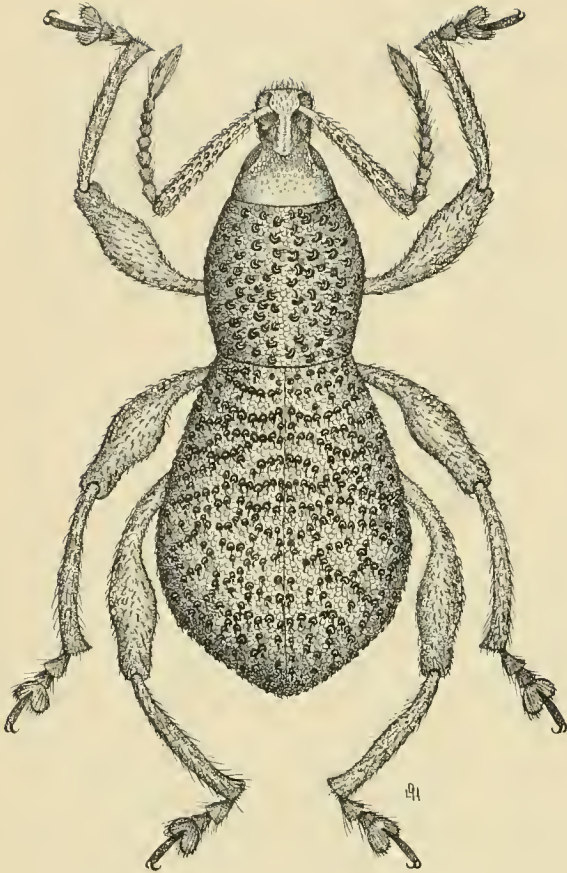


Fig. 3. *Kietana episomoides* Hllr.

brown clothed with white scales and setae, tarsi black; ventral area and ventrites with white scales and setae.

Length 9.8 mm; breadth 4 mm.

Type locality: Bougainville, Kieta (Dr. Schlaginhaufen) 1908-5 *typus*, 1908-5 Staatl. Museum für Tierkunde, Dresden.

Kietana gressitti n. sp.

Fig. 4

Derm black with small pale greenish scales, pronotum with a narrow median strip of scales; elytra, legs, and ventral surface with small groups of green scales.

Head rugose with small punctures on apical portions of frons, diminishing toward base; eyes large, slightly convex, lateral and in contact with rostral suture; rostrum longer than head, dilated at genae, dorsum and apical declivity punctate, with a slight elevation and fovea at junction of two carinae and declivity. *Antennae* scape widening gradually from base to apex, punctures deep, clothed with long recumbent brownish setae and

a few green scales; scape reaching the anterior two-fifths of prothorax; funicle slightly longer than scape, all segments pyriform, 1 a little larger than 2. *Prothorax* longer than head and rostrum combined; widest at middle, sides practically parallel; truncate at base and apex; disc convex, highest in middle, sloping to apex and base, closely set with rounded granules, from one side of which issues a small brown seta, giving granules a lunate appearance, green scales sparsely placed between granules, median area more heavily covered with scales. *Elytra* broadly ovate, widest behind middle, dorsum convex highest before middle, punctures in striae, granules in main, along intervals, some small ones in striae paths; small brown setae arise from side of granules; some scales between granules of intervals; setae long, brownish and recumbent on precipitous declivity. Underside, prosternum, mesosternum, metasternum, ventrites 1 and 2 sparsely clothed with green scales and short, white setae.

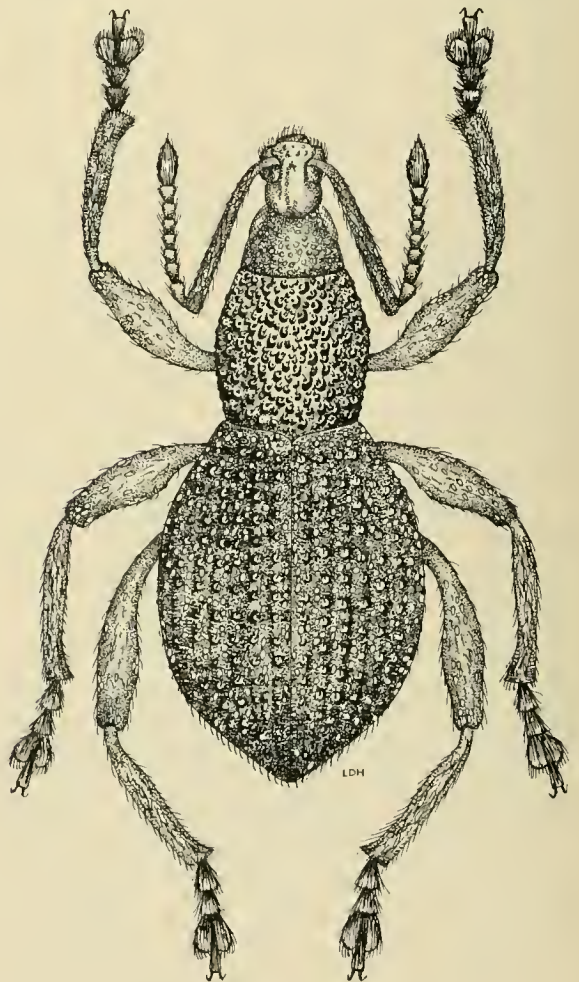


Fig. 4. *Kietana gressitti* n. sp.

Legs, femora, tibia, and coxa reddish-brown, tarsus black with white recumbent setae.

Length 8.0–8.1 mm.; breadth 4.0 mm.

Type locality: Solomon Islands: Holotype Guadalcanal, Gold Ridge, 500 M. June 24, 1956, (J. L. Gressitt). One paratype, same data as the Holotype; one paratype Guadalcanal Is. Gold Ridge, March 21, 1955, E. S. Brown. Holotype, deposited in the Entomological Collection Bishop Museum, Honolulu, Hawaii; one paratype in the Entomological Collection, British Museum of Natural History, London; and one paratype in the Entomological Collection, Brigham Young University, Provo, Utah.

Remarks: The species *gressitti* is black with a narrow prothorax, similar in shape to that of *tessellata*, but is larger, with green scales, and more deep punctures on the dorsal area of the rostral declivity. *K. aluensis* in contrast to *gressitti* has a more rugose and rounded prothorax, and is larger with conspicuous white scales on body and legs. The rostral carina and elevation at top of the declivity is distinctive in each of these species.

GENUS CELEUTHETES SCHONH.

Schöenheer. Gen. Spec. Curc. VII, 1, 1843, p. 250.

Rostrum as long as the head, robust, abruptly declivous dorsally at apex; declivity without scales or a dorsal elevation, scrobes deep, triangular, dorsal area shallowly excised, narrowest part two to three times as wide as apex of scape. *Antennae* submedium, rather long and slightly robust, scaled and with setae; scape subcylindrical, straight except for slight arch at base; funicle segments 1-2 elongate, 1 longer than 2, 3-5 subpyriform, 6-7 subglobular, club oval. *Eyes* rather large, round, protruding. Prothorax subcylindrical, slightly rounded at sides; truncate at apex and base. Elytra short and moderately rounded; concave dorsally in ♂ or regularly convex in ♀. Elytra not wider than prothorax at base, with shoulders rounded or rectangular; often granular, but without conical tubercles. Mesosternal process longer than shortest distance between coxae. Corbel of posterior legs cavernous and claws on tarsus free.

Celeuthetes paganus Gyll

Gyllenhal in Schönh. Gen. Spec. Circ. II, 2, 1834, p. 539.

Fig. 5

Derm reddish black, with small white scales and setae which arise from small polished granules.

Head and rostrum as long as prothorax; *rostrum* with a furrow, narrowest part three times as wide as apex of scape, declivity without scales or a dorsal elevation; a small fovea at base of rostral groove; rostral sulcus extending laterally and forward to anterior margin of eyes; rostrum two-thirds as long as head. *Antennae* scape slightly bowed, same diameter throughout, extending to anterior one-third of prothorax; segments 1-2 of funicle as long as 3-6; segments 3-7 globoid, eyes large, round, flattish and placed well down on lateral portion of head. Prothorax as long as wide; apex slightly concave, base truncate, trans-

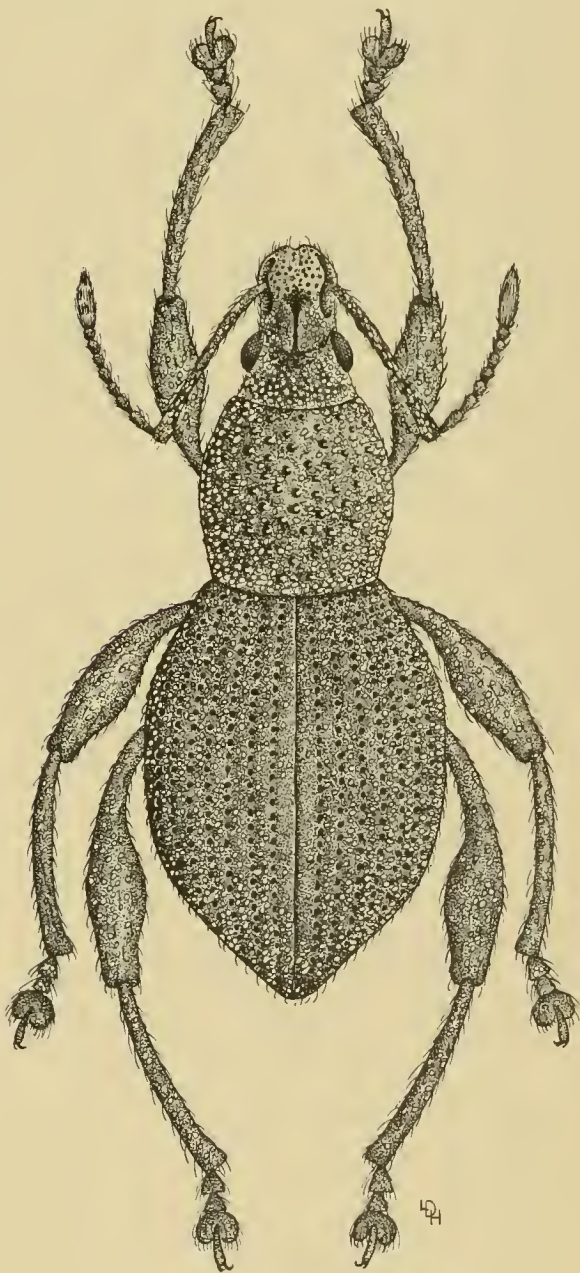


Fig. 5. *Celeuthetes paganus* Gyll.

versely convex, widest at middle, disc and lateral portions granulate and punctate. *Elytra* widest at middle, one-fourth longer than wide, stria 12 abbreviated; intervals on disc twice as wide as striae, interval 6 units just back of humerus with 5 and 7 forming a low obscure carina, (there is also a union of these intervals at the declivity which results in forming a low keel which extends to the apex) shallow closely set punctures in striae, small shining granules with decumbent setae on intervals, scales and setae abundant on declivity down to apex. *Legs* reddish, thickly covered with white scales and setae. Prothoracic coxae large and narrowly separated, ventrites 1-2 rugose laterally free from punctures and setae in middle; 3-5 free from scales and setae.

Length 7.8 mm; breadth 3.2 mm.

Type locality: Santa Cruz Islands, Vanikora Island. Specimen studied: One from the Solomon Islands, Guadalcanal, Teneru River, (D E. Beck), 1944. Bougainville Is. 2 specimens, June 5, 1944, (A. B. Gurney); two specimens, June 30, 1956, Simba Mission (E. J. Ford, Jr.).

The species assigned to *Celeuthetes* are widely distributed from Australia to New Hebrides, New Guinea, Bismarck, and Solomon Islands. The species *paganus* is the only member of this genus thus far reported from the Solomon Islands.

GENUS *ATACTOPHYSIS* HELLER

Heller, Verh. Naturf. Ges. Basel XLV, 1934, p. 9.

Body depressed, with few scales, *rostrum* as long as wide, dorsal without keel, basal sulcus deep and crescent shaped, eyes not in contact with rostrum, due to deep sulcus. *Antennae* scape cylindrical, straight, apically knot shaped; not extending to middle of prothorax, segments 1-2 of funicle elongate; equal in length to segments 3-5 combined; club as long as segments 5-7 combined. *Prothorax* as wide as long, base and apex truncate, convex transversely; with median longitudinal elevation and shallow close set punctures. *Elytra* with eleven striae, depressed, heart-shaped, humerus equal to base of prothorax, sloping from base to obtuse point, in contact with coxa of metathoracic leg, apex acuminate. Femora extending slightly beyond apex of elytra.

ATACTOPHYSIS CORDATA HELLER

Heller, Verh. Naturf. Ges. Basel XLV, 1934, p. 9.

Fig. 6

Derm black with bluish-white scales, sparse white setae, prothorax finely punctuate, elytra

with rows of granules between interspaces.

Head as long as rostrum, vertex rugose; rostral sulcus deep, crescent shape; antennae scape narrow, except at apex, practically devoid of scales and setae, funicle segments 1-2 as long as 3-5, club as long as 5-7; funicle devoid of any vestiture; rostral base broad with deep punctures, no carina, but with a slight elevation at rostral declivity, scrobes large, separated dorsally by about width of apex of scape. *Eyes* lateral, round, flattish and contiguous with rostral sulcus. *Prothorax* greater in breadth than length; base and apex truncate, disc convex transversely punctures shallow and irregular in placement; low median carina, a few white scales on lateral margin, body scales denuded, except for a few scattered bluish and white ones. *Elytra* 4 mm in width at base, 7 mm in greatest width and 7.6 mm in length; disc flat, heart-shaped; striae consisting of shallow punctures and rows of small polished granules. The 11 intervals smooth, on discal area practically free of scales; posterior margin emarginate, gentle slope at declivity, covered with more scales and deeper punctures; anterior lateral margin of metathorax impressed and with deep punctures, lateral margin of elytra in contact with coxa of metathorax leg. *Legs* elongate, prothoracic very narrowly separated; metathoracic coxa widely separated. Ventrites 1-2 rugose laterally with fine wavy lines in medial area, 5 greater in width than 3-4 combined.

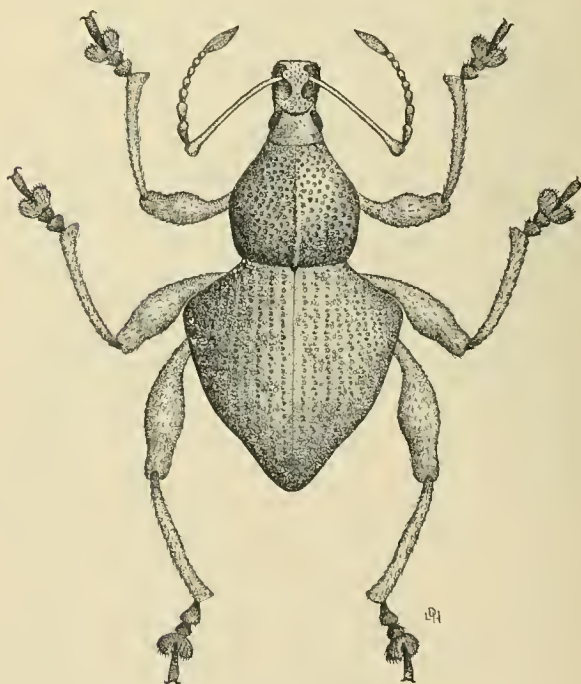


Fig. 6. *Atactophysis cordata* Hllr.

Length 13.5 mm; breadth 7 mm.

Type locality: Solomon Islands (T. Bödecker) *Typilus*, Städtl. Museum für Tierkunde, Dresden.

The genus *Atatophysis* is characterized by its elytra which are flattened and heart-shaped. It is widest where the lateral margin of the elytra comes in contact with the coxa of the metathoracic leg. The 11 striae, the rows of small, polished granules, the smooth intervals, shallow punctures and acuminate apex of the elytra, along with the deep rostral sulcus, deep punctures on the base of the rostrum, slender scape of the antennae, and the flat eyes which come in contact with the lateral extension of the rostral suture are all outstanding characters. I have been unable to compare this genus with *Atactus* because of the lack of correctly determined specimens.

GENUS PLATYACUS FAUST (1897)

Platyacus Faust, 1897, Stett. Ent., Zeit. 58: 236, 270

Colposternum Heller, 1910, Wien., Ent. Zeit. 29: 191

Hoplotrigonops Heller, 1934, Verh. Naturf. Ges. Basel 45:21

This genus, peculiar to the Solomon Islands, is characterized by the presence of several small teeth on the femora, a distinct modification of the fourth ventrite, (Figs. 1-4), a sinuation of the front margin of the prosternum, the steep frontal part of the head, with the eyes closely approximate, and a long slender rostrum with an elevated straight keel.

Through the kindness of Dr. Wilhelm Gotz of the Dresden Museum I have seen cotype specimens of *Platyacus subalatus* (Hllr.); *P. laticollis* Hllr.; *P. malachiticus* Hllr.; *P. nigrocristatus* Hllr.; *P. decoratus* Fst.; *P. websteri* Fst.; *Hypotactus ruralis* (Fst.); *H. papillatus* (Fst.); *H. novobritannicus* var. *suturalis* Hllr.; and *Paratactus carbunculus* Hllr.

Drawings have been made of all the species

of *Platyacus* as listed above, also of *Hypotactus ruralis*, *papillatus*, and *novobritannicus* var. *suturalis* Hllr., and *Paratactus carbunculus* Hllr.

Both Faust and Heller were not sure as to the generic characters of some of the species of this complex. Marshall's analysis of the genera *Platyacus*, *Colposternum*, and *Hoplotrigonops* resulted in his concluding that the two latter ones were synonyms of *Platyacus*.

He also observed that the two Faust species *Platyacus ruralis* and *papillatus* were not congeneric with the genotype of *Platyacus* (*websteri* Fst.). "They differ from *Platyacus* in the much shorter rostrum, the truncate (not sinuate) front margin of the prosternum, the gently sloping frons, the width of which is as great as, or greater than, the length of an eye, and the more lateral position of the eyes. The female has only four visible ventrites." Marshall thus erected the genus *Hypotactus* for these two species. I have concluded, from my study that *P. novobritannicus* var. *suturalis* Hllr. also belongs in *Hypotactus*.

The species of *Platyacus* are, at this stage of our knowledge, recorded only from the Solomon Islands, while species of *Hypotactus* have been reported only from the Bismarck Archipelago. The cotype specimen *Hypotactus novobritannicus* var. *suturalis* Hllr. bears a locality label "N. Pommern" now known as New Britain. The other two species *ruralis* and *papillatus* are also from New Britain.

This leaves the species *carbunculus* Hllr. which does not belong in *Platyacus*, but has been assigned to *Paratactus* by Marshall.

This study is concerned only with the celeuthetini of the Solomon Islands; but since *Hypotactus ruralis*, *papillatus* and var. *suturalis* and *Paratactus carbunculus* have been dealt with as species of *Platyacus* or in genera now considered as synonyms of *Platyacus* and since they are not well represented in most entomological collections, drawings of cotypes from the Dresden Museum are included. It is my belief that illustrations of rare species will be an aid in future studies of the weevils of the Solomon Islands.

KEY TO THE SPECIES OF PLATYACUS

Sir Guy Marshall's Key to the species of *Platyacus*. Marshall notes that the species *subalatus* and *laticollis* of this Key were known to him from the description only.

1. (4) Prosternum with a projecting tooth on each side of the apical sinuation.
2. (3) Elytra with the dorso-lateral margin raised into a comb-like ridge in the middle two-thirds, the intervals without granules; funicle longer than the scape (Bougainville I.) Fig. 7. *subalatus* Hllr.

3. (2) Elytra without such a ridge, the intervals granulate; funicle shorter than the scape (Bougainville I.) Figs. 8, 14 *laticollis* Hllr.
4. (1) Prosternum without teeth on the front margin.
5. (20) Rostrum slightly widening apically, or at least parallel-sided, the scrobes comparatively large, ill-defined behind, the narrowest space between them not wider than a scape.
6. (7) Elytra with a distinct callus on intervals 4 at the top of the declivity, the apical lateral margin deeply excised in ♀ (Kolombangara I.) Figs. 9, 14 *kolombangarae* Mshl.
7. (6) Elytra with no posterior callus in interval 4, the apical lateral margin straight or shallowly sinuate.
8. (11) Elytra with a callus or short ridge at the top of the declivity on interval 5.
9. (10) Prothorax rounded laterally, flattened on the disk; tibiae with a fine dorsal carina on the basal half; tarsi with joint 2 transverse; elevations on interval 5 of the elytra without suberect black setae; length 6.0–7.5 mm. (Bougainville I.) Fig. 10 *malachiticus* Hllr.
10. (9) Prothorax parallel-sided in the basal half, transversely convex on the disk; tibiae without any dorsal carinae, tarsi with point 2 somewhat longer than broad; elevations on the elytra with short black suberect setae; length 4.5–5.0 mm. (Bougainville I.) Fig. 11 *nigrocristatus* Hllr.
11. (8) Elytra without any trace of a callus or ridge on interval 5.
12. (19) Scape rapidly widened close to the base and then parallel-sided to the apex, compressed, with the lower edge sharply carinate.
13. (14) Elytra with bands of yellowish-green scales; a complete, basal band which emits three backward elongations along the suture and the sixth intervals, a much shorter band behind the middle extending to stria 4 and broadly interrupted at the suture, and a band covering the whole apical area except the suture; scape narrower and dilated apically (Isabel I.) Figs. 12, 14 *decoratus* Fst.
14. (13) Elytra without bands, the green or yellowish scales more generally distributed; scape thicker, almost parallel-sided from near the base to the apex.
15. (16) Elytra with the scales sharply confined to the intervals, the bare striae (as broad as the intervals) appearing like black stripes; ventrite 4 of ♀ with the processes at the external apical angles only half as long as the median process (Alu I.) Fig. 13 *websteri* Fst.
16. (15) Elytra with the green scales covering the septa between the punctures in the striae, the bare punctures producing a tessellated effect, with no sign of stripes; ventrite 4 of ♀ with the external apical processes nearly as long as the median process.
17. (18) Prothorax rounded laterally (Florida I., Giza I.) Fig. 15 *leveri* Mshl.
18. (17) Prothorax parallel-sided in the basal half (Fauro I.) *fauronus* Mshl.
19. (12) Scape more slender, gradually widening from base to apex, not compressed, nor carinate on the lower edge (Bougainville I.) Fig. 14 *minor* Mshl.
20. (5) Rostrum gradually narrowing from base to apex, the scrobes small, ovate, sharply delimited behind, the space between them much wider than a scape (Bougainville I.) *narinus* Mshl.

Platyacus subalatus Hllr.

Heller, Wien. Ent. Zeit, XXIX, 1910, p. 194

Fig. 7

Derm black, except the proximal portions of the femora which are red, with small green and white scales, irregularly and sparsely placed on dorsum of body, antennae and femora.

Rostrum much longer than head, parallel-sided dorsum narrow, carina with small elevation at top of declivity; separated from head by sulcus which extends lateral and anteriorly to scrobes; antennae long, funicle reaching middle of prothorax bowed slightly, same diameter throughout, except for rounded distal end, funi-

cle segments all elongate. *Prothorax*, prosternum with a projecting tooth on each side of apical sinuation, wider than long, widest posterior of middle, truncate at base and apex, slight constriction at apex; disc flat, rugose, with varying-sized granules, no punctures or setae, no marked median area, and few small scales. *Elytra* with dorso-lateral margin raised into a comblike ridge in middle two-thirds, intervals without granules, striae punctured, short white setae at apex. *Legs*, femora red in color on proximal and club areas, reaching just beyond apex of elytra and with small tooth on each femora. Tibia straight with long white setae. Ventral body and ventrites devoid of scales, ventrites with short suberect setae, ventrite 5 longer than 3-4.

Length 9.8 mm; breadth 5.2 mm.

Type locality: Bougainville Island-Kieta. The above description was made from the following specimen: Bougainville - Kieta (Dr. Schlaginhaufen), 1908-5; Typus, Staatl. Museum für Tierkunde, Dresden. Other specimens studied: Solomon Islands: Bougainville Islands, Kokure, Nr. Crown Prince Ra. 900 M. VI-8 1956 (J. L. Gressitt).

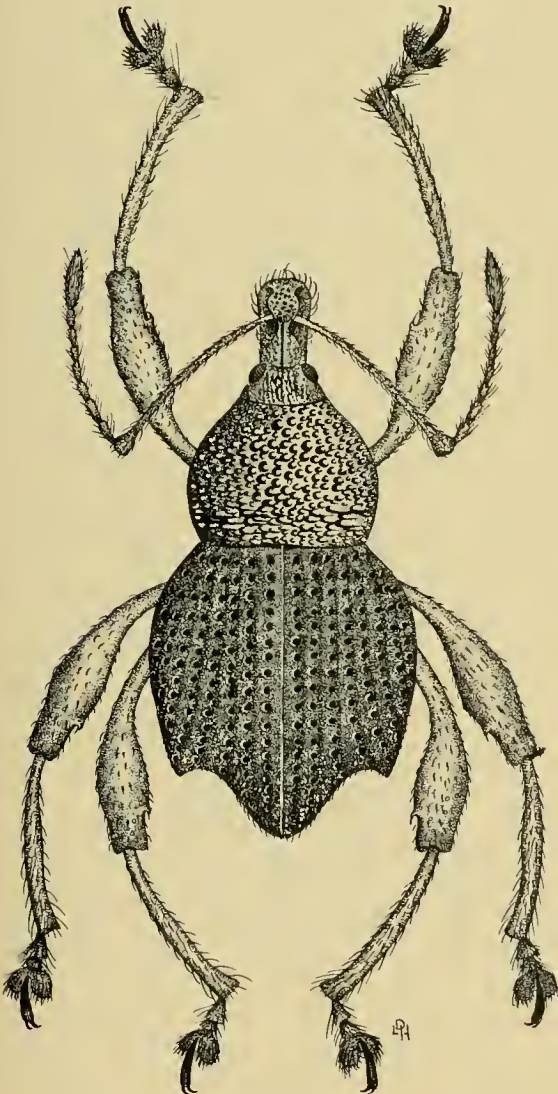
Platyacus laticollis Hllr.

Heller, Wien. Ent. Zeit. XXIX, 1910, p. 193

Fig. 8, 14

Derm black with white scales, some iridescent.

Rostrum twice as long as head, narrow in middle, expanded at apex, carina ending in U-shaped elevation at declivity which is finely punctuate. Sulcus separating rostrum from head circular in shape. *Antenna* scape enlarged at distal end, reaching middle of prothorax, funicle shorter than scape, segments elongate, club as long as segments 5-6-7 combined. *Prothorax*, prosternum with projecting tooth on each side of apical sinuation; more than one-fourth wider than long, widest back of middle, base truncate, apex concave, disc flat, slightly concave along medial area, with granules. *Elytra* widest near base, broadly ovate and acuminate behind, intervals 3-4 slightly elevated at declivity, punctures along striae and granules on interval, granules on intervals 3-4 at declivity prominent, with short setae, white scales in irregular transverse rows across elytra. *Legs*, femora not reaching apex of elytra, one large and several smaller teeth on each of femora, no scales, but few setae on underside of body; fourth ventrite of female deeply bimarginate forming a median lobe as shown in Fig. 14, segment 3 is sparsely covered with setae.

Fig. 7. *Platyacus subalatus* Hllr.

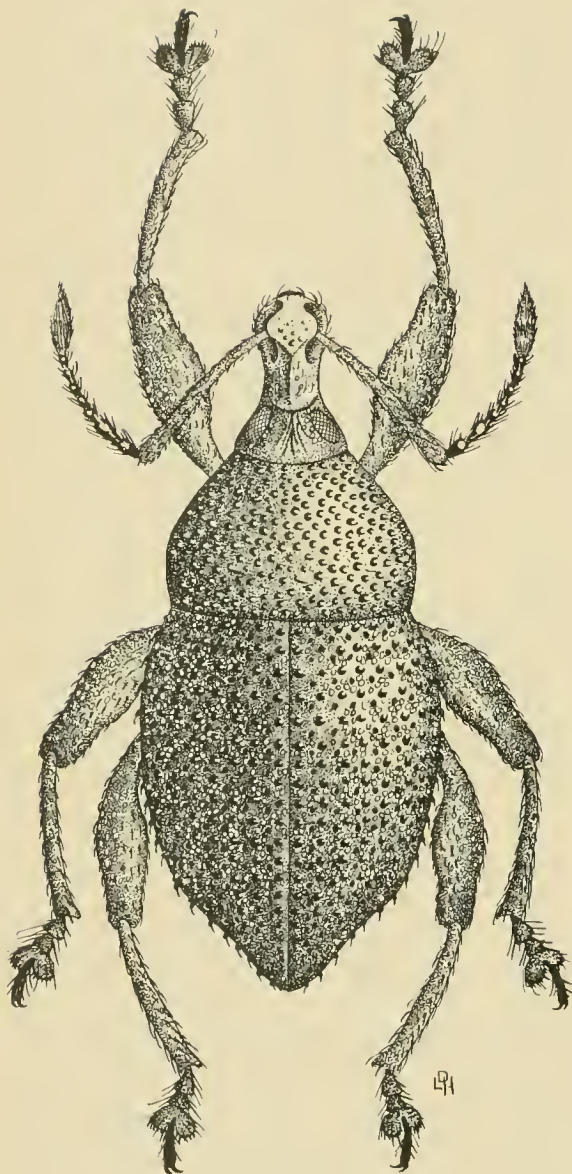
Platyacus kolombangarae Mshl.

Marshall, Otiorrhynchine Curculionidae, Tribe Celeuthetini, 1956, pp. 68-70, Fig. 25, British Mus., Nat. Hist.

Fig. 9

Derm black with dense green scales, except in the middle of the venter.

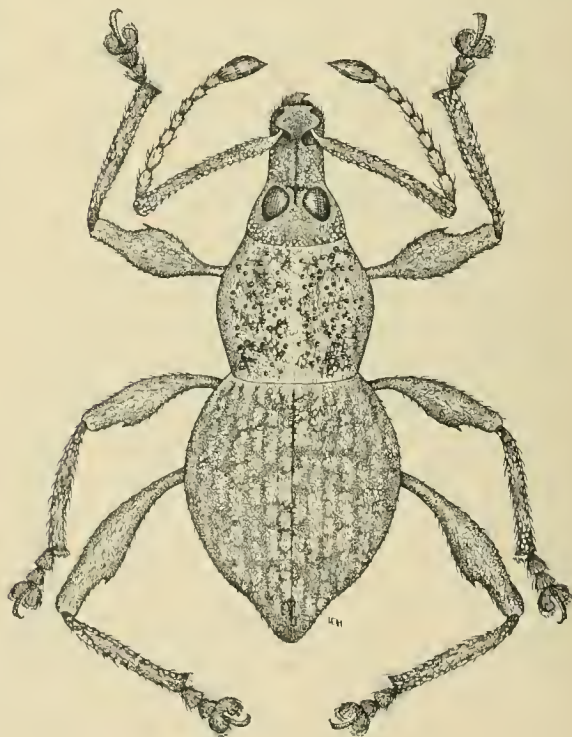
Rostrum narrow, carina ending at declivity without an evident elevation, sulcus V-shaped; antennae wide from origin to apex, slightly bowed, with dense green scales and decumbent black setae, scape reaching slightly beyond middle of prothorax; funicle a little longer than scape, segments elongate, especially 1-2. *Prothorax* wider than long, rounded laterally, slightly constricted near apex, widest behind middle, base and apex truncate, disc convex with small black granules and dense green scales, median area more densely set with scales, punctuate on pleurae. *Elytra* of female ovate, acuminate behind with lateral margin sinuate near apex, a distinct sub-apical elevation near apex of interval 4; male without callus, or margin sinuation, shortly acuminate behind and with apex produced downward; dorsum convex, striae with deep naked punctures, intervals between striae covered with dense green scales which obscure

Fig. 8. *Platyacus laticollis* Hllr.

Length 10.2 mm; breadth 5.0 mm.

Type locality: Bougainville Island. The above description from one specimen from Salamo Inseln-Kieta 1910, 12-typus-Staatl. Museum für Tierkunde, Dresden.

Remarks: The fourth ventrite of *kolombangarae* Mshl. is very different to that of *laticollis*. This is a good ♀ character which may prove to be of aid in separating species of this genus. Fig. 26: p. 70 of Marshall's "Otiorrhynchine, Curculionidae of the tribe Celeuthetini" is mislabeled, it should be venter of *Platyacus kolombangarae* Mshl.

Fig. 9. *Platyacus Kolombangarae* Mshl.

small granules with short setae. *Legs*, black and reddish-brown, all femora with a small tooth, tibia straight. Covered dorsally with green scales. Ventrites without scales, except 1 and 2 with scales laterally and along posterior margin of 2. Fourth ventrite of female modified as shown by Sir Guy Marshall.

Length 5-6 mm; breadth 3.0-3.6 mm.

Type locality: Solomon Islands: Kolombangara Island. Locality of specimens studied: New Georgia Group, Kolombangara, Island Kukundu, S. W. Coast 1-12 M, 10 VII, 1959, (J. L. Gressitt). New Georgia Group: Nr. Ego, 1-25 m. July 16, 1959, (J. L. Gressitt) *Freycinetia*. Solomon Islands: Kolombangara-Iri-iri, 27 VII, 1958, (P. G. Fenemore); Vella Lavella, Tiopari, 26 VII, 1958, (P. G. Fenemore); Choisaul, Luti, 1 VIII, 1958, (P. G. Fenemore).

Remarks: Dr. Gressitt collected specimens of *kolombangarae* on the following plants; *Calophyllum*, *Freycinetia*, *Flagellaria*, and the palm.

Platyacus malachiticus Hllr.

Heller, Wien. Ent. Zeit. XXIX, 1910, p. 192

Fig. 10

Derm black with green and some iridescent scales.

Rostrum short, expanded some at apex, carina acute, small elevations at declivity, declivity scaleless, and punctate; antennae scape slightly bowed, same in diameter throughout, reaching beyond the middle of prothorax, punctate and covered with scales and decumbent setae; funicle segments elongate. Two-longer than 1. *Head* shorter than rostrum, rugose and punctate to the apex; eyes round, slightly convex, frons, between eyes as wide as diameter of eye; sulcus separating head from rostrum circular. *Prothorax* 3.2 mm in breadth, 2.3 mm long, constricted near apex, widest a little behind middle, truncate at base, slightly concave at apex, punctate on pleurae, disc flat, with black shiny granules and punctures obscured by green scales. Prosternum has a slight sinuation and small projection which resembles a tooth. *Elytra* broadly ovate, widest before middle, elevation on interval 5, without subrect black setae, sharply acuminate behind narrow declivity, dorsum only slightly convex transversely; shallow striae with punctures, intervals with cluster of scales and small black granules, small recumbent white setae. *Legs* proximal portion of femora reddish; anterior femora with one large and several small teeth. Ventral surface with setae devoid of scales; ex-

cept lateral portion of metasternum; ventrites scaleless, 4-3 times as long as 3, normal in shape.

Length 9 mm; breadth 5.0 mm.

Type locality: Solomon Islands, Bougainville Islands. The above description from one specimen from Bougainville Island-Kieta (Kapt. Kurtz). 1908-3-Typus Staatl. Museum für Tierkunde, Dresden. Other specimens studied: Bougainville Is.-(S.) Kieta, XI, 30 1959, (T. C. Maa), Bishop Museum Bougainville Is. Pukpuk, Nr. Kieta VI 26, 1956, (E. J. Ford, Jr.). Bougainville Is.-Kaure 690 m. VI -8-18-1956 (J. L. Gressitt). Kokure, Nr. Crown Prince Ra. 900 M. VI-10-1956 (J. L. Gressitt).

Remarks: The specimen of *malachiticus* from Dresden has a small projection on the proster-

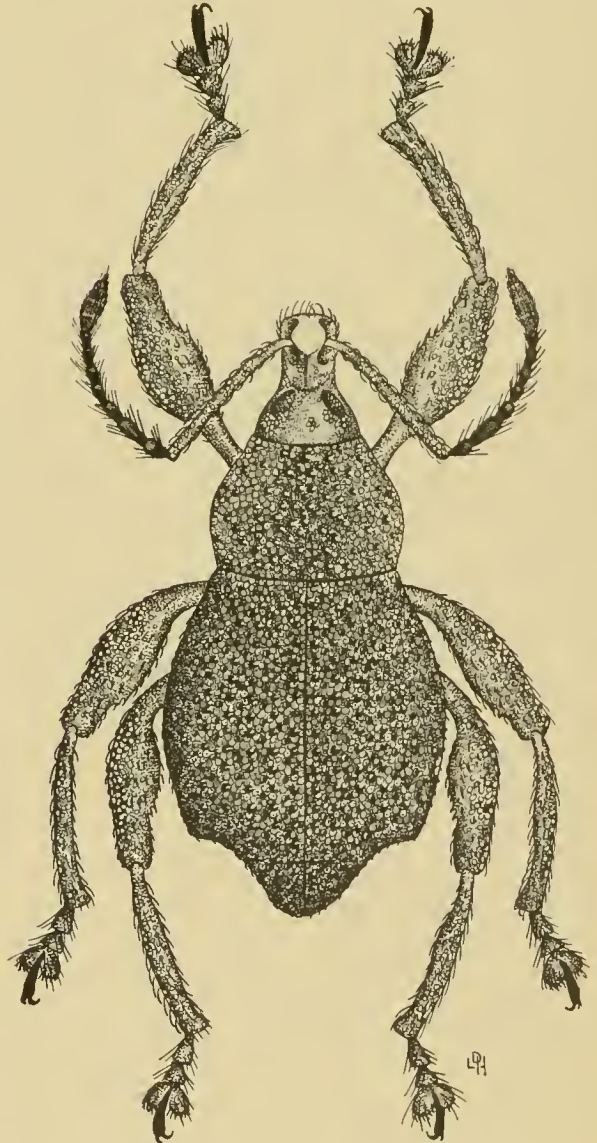


Fig. 10. *Platyacus malachiticus* Hllr.

nal apical sinuation, likewise, some specimens collected by Dr. Gressitt. This should be considered when using the above key by Sir Guy Marshall.

Platyacus nigrocristatus Hllr.

Heller, Verh. Naturf. Ver. Basel XLV, 1934, p.22

Fig. 11

Derm brownish, black, with dense white scales. *Rostrum* a little longer than head, parallel sides, carina distinct, scales dense with small black granules showing through, slight elevation at declivity which is reddish-brown with sparse white setae, scrobes small separated by a greater width than diameter of antennae scape. *Antennae* slightly bowed, gradually increasing in diameter to apex, densely covered with white scales and decumbent black setae, extending beyond middle of prothorax, funicle a little longer than scape; segments 1-2-3 as long as segments 4-5-6-7 combined. *Head* densely covered with scales, a frontal carina which meets rostral carina at curved sulcus; punctate extending to apex of head, granules interspersed among scales; eyes large, ovate, space between them less than diameter of eye. *Prothorax* 1.6 mm. long, 1.8 mm. in breadth, parallel sided in basal half, transversely convex on disc with granules and punctures, scales on septa around punctures (except in medial area which is sparsely covered); base and apex truncate, pleurae punctate and densely covered with scales; a short white setae issuing from each puncture. *Elytra*, greatest width just before middle, shallow striac with punctures similar to those on prothorax; white scales on septa between punctures and on intervals; slightly convex at middle becoming concave between black elevations on fifth interval, shortly acuminate behind with apex produced downward. *Legs* brownish covered with white scales and setae; all femora with a large brown-colored tooth; venter and ventrites 3-4-5, with white decumbent setae, ventrite 4 of ♀ sculptured similarly to that of *websteri* Faust.

Length 5.0-6.8 mm; breadth 3.0-4.0 mm.

Type locality: Solomon Islands, Bougainville Islands. This description was made from one specimen from Bougainville, 30-5-60, 1926-5 *Platyacus* (*Hoplotrigonops*) *nigrocristata* L'N H typus 33 (the genus and species is in Heller's hand writing) Staatl. Museum für Tierkunde, Dresden.

Other specimens studied: Solomon Islands: Bougainville Is. (5). Kieta, XI. 27, 1959, (T. C. Maa). Bishop and Simba Mission, June 29, 1956, (E. J. Ford, Jr.).

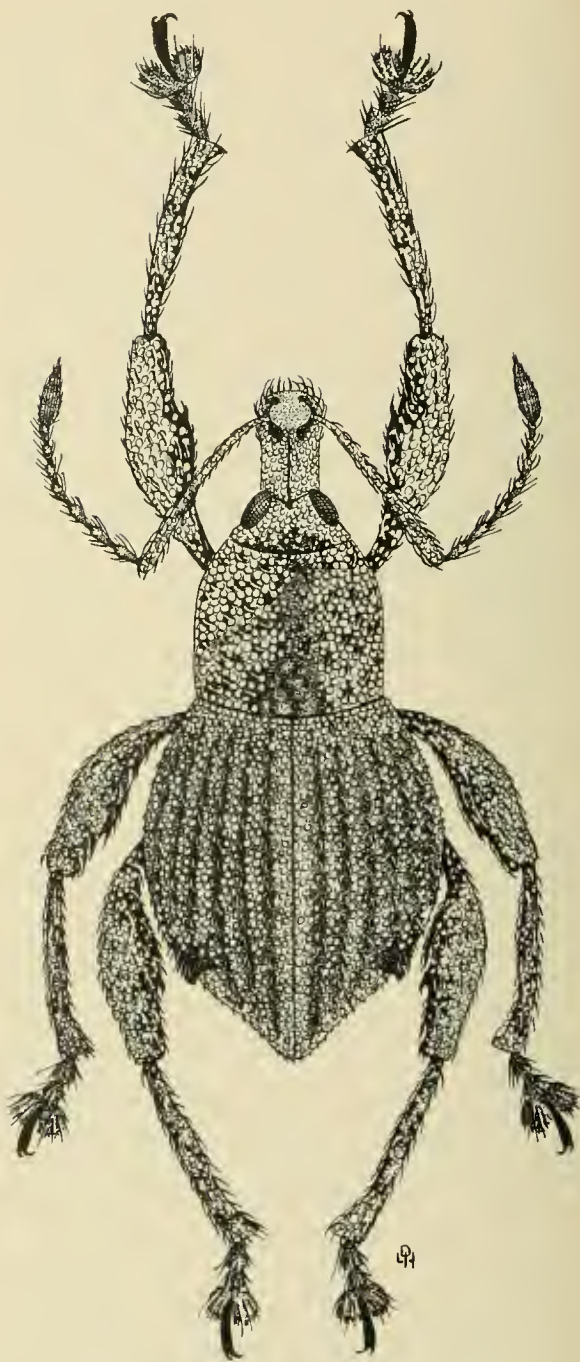


Fig. 11. *Platyacus nigrocristatus* Hllr.

Platyacus decoratus Fst.

Faust, Stett. Ent. Zeit. LVIII, 1897, p. 272

Fig. 12

Derm with black small blue-green and yellowish scales.

Rostrum, sides parallel, one and one-half time as long as head, carina with small elevation at declivity; antennae scape narrow at origin, en-

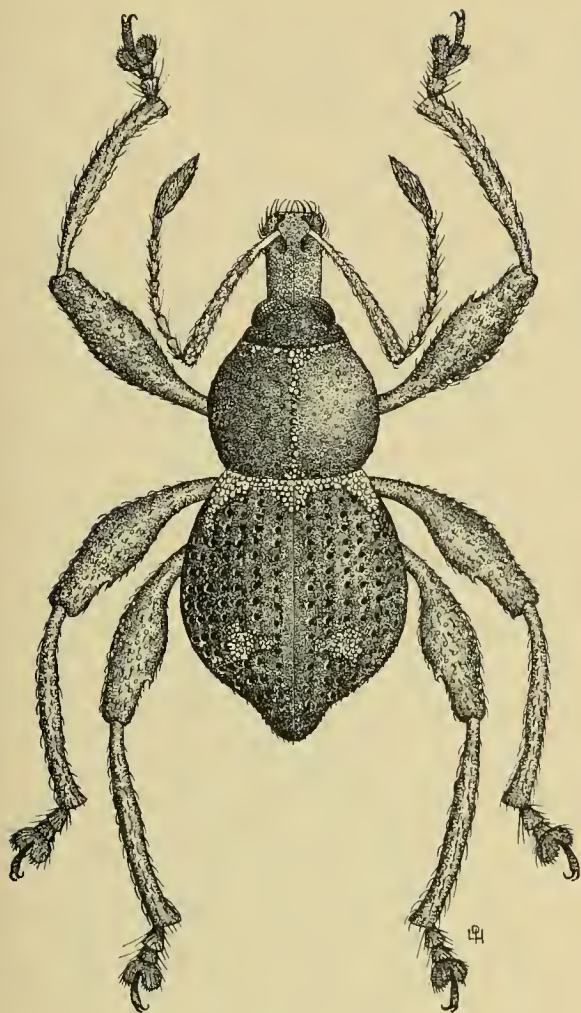


Fig. 12. *Platyacus decoratus* Fst.

covering entire apical except suture, striae with larged at apex, reaching anterior half of prothorax, funicular segments 1-4 pyriform, 5-6-7 diameter equal to length, club slightly longer than preceding three funicular segments. *Head* short, with small blue scales and irregular wavy elevated lines from between eyes to apex, frons between eyes narrower than width of eye. Eyes frontal and moderatley convex. *Prothorax* wider than long, base and apex truncate, slightly constricted near apex, widest before middle, transversely convex, disc rather rugose, granules showing through scales which obscure punctures. Medial line with dense green scales. *Elytra* ovate, sharply acuminate especially in ♀ with bands of yellowish green scales, a complete basal band from which extends three backward elongations along the suture and 5-6-7 intervals, a shorter band behind middle extending to stria 4 and broadly interrupted on suture and a band

punctures, septa and intervals with small blue and green scales. ♀ with tuft of setae on suture of declivity. Small granules with short setae on intervals. *Legs* black with blue and green scales on femora with a large tooth and several smaller ones. Tibia slender, straight, and long. Venter covered with scales, except middle area of ventrites 1-2 and all of 3-4-5. Ventrites 4 with modified fourth segment (Fig. 14).

Length 5.1-6.5 mm; breadth 2.9-3.2 mm.

Type locality: Solomon Islands: Isabel Island. The above description was made from one specimen with the following notation on the small gold-colored square label on the pin - Isabel I. (Webster). *Decoratus* Faust; Coll. J. Faust, Ankauf 1900 - Typhus - Staatl. Museum für Tierkunde, Dresden. Other specimens studied: Solomon Islands - New Georgia Group, N. Georgia Is. - Munda 1 - 30 M. VII - 15 - 1959 (J. L. Gressitt) *acalypha*.

Remarks: The fourth ventrite of the ♀ is distinctive, Fig. 14.

Platyacus websteri Faust

Faust, Stett. Ent. Zeit. LVIII, 1897, p. 270

Fig. 13

Derm black, clothed with a mixture of green-white and blue scales or entirely all blue scales.

Rostrum parallel-sided and almost twice as long as wide; dorsum narrow with a central carina, bordered on each side with a small carina, very small elevation at top of declivity; separated from head by a sulcus. Carina of rostrum continuous with carina of frons. *Antennae* long, scape reaches beyond three-fifths of prothorax; slightly curved, as wide at base as apex, funicle segments elongate, segments 1-2 as long as 3-4-5 combined, club long and slender; scales on dorsal portion of scape. *Prothorax* wider than long, widest at middle, truncate at base and apex, slightly constricted at apex; dorsum flat toward base, closely set with small granules and punctures, median line densely covered with scales. Prosternum without teeth on front margin. *Elytra* widest at anterior third, gently sloping to apex, 10 striae with deep punctures, distinctly separated from intervals which are covered with rows of scales. Declivity and apex practically devoid of setae. *Legs*, femora reaching tip of elytra, basal portion of femora narrow, club not robust, teeth on all femora, tibia straight, ventral surface of body covered by scales except median portion of ventrites 1-2 and all of 3-4-5 with densely covered fine setae.

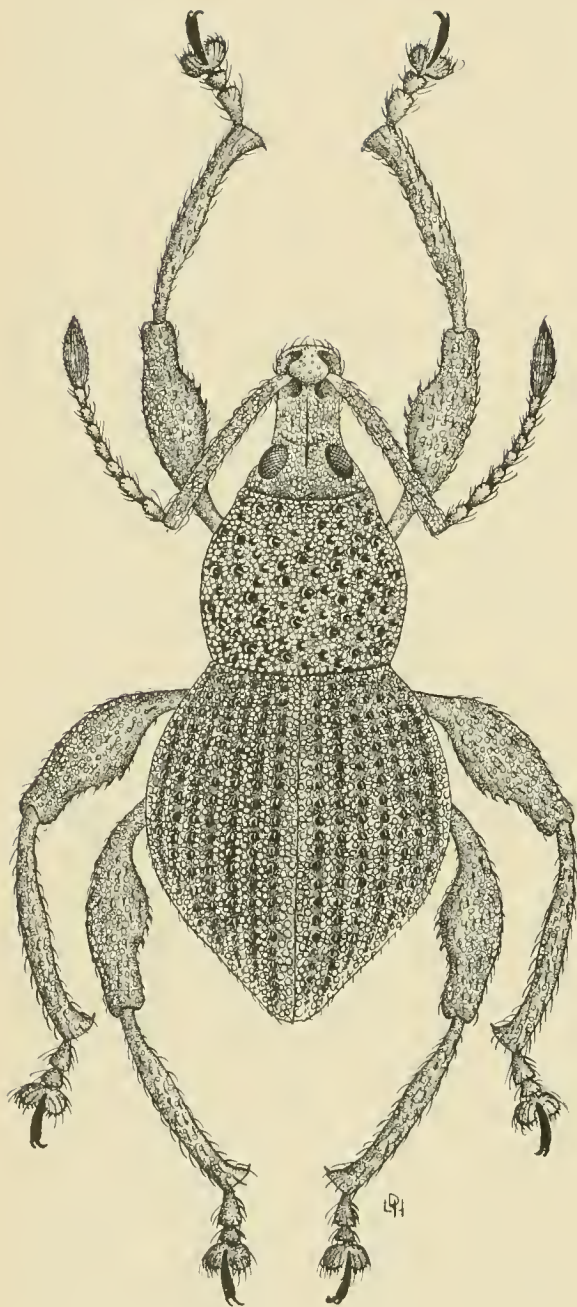


Fig. 13. *Platyacus websteri* Faust.

Length 6.0-6.2 mm; breadth 2.9-3.0 mm.

Type locality: Solomon Islands: Alu Island (Webster). The above description was made from two specimens; one with a small gold-colored square, Alu I - Shortland Is. (Webster); *websteri* Faust; Coll. J. Faust, Ankauf 1900; *Typus*, Staatl. Museum für Tierkunde, Dresden, one with small gold-colored square; *Solomonus*

? *websteri* Faust; Coll. J. Faust, Ankauf, 1900, *Typus*, Staatl. Museum für Tierkunde, Dresden. Other specimens studies: Solomon Islands; Buka Islands: Gagon, 40 M. VI - 15 - 1956 (J. L. Gressitt).

Remarks: The statement in the key, "ventrite 4 of ♀ with the processes at the external apical angles only half as long as the median process," could not be observed on specimens listed above. The one specimen labeled "*Solomonus*?" is well marked with blue scales in contrast to the specimen labeled "Alu I - Shortland Is." which is covered with scales colored green-white and with some blue ones.

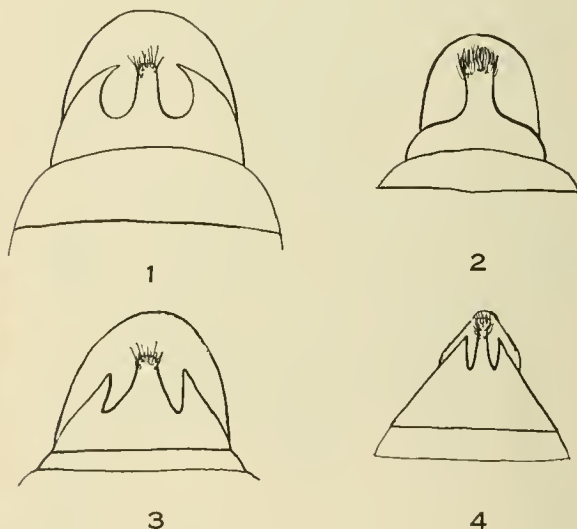


Fig. 14. Female ventrites of species of *Platyacus*. (1) *P. laticollis* Hllr.; (2) *P. Kolombangasae* Mshl.; (3) *P. decoratus* Fst.; (4) *P. minor* Mshl. The fourth ventrite is structurally distinctive.

GENUS *HYPOTACTUS* MARSHALL

Marshall, the Otiorrhynchine Curculionidae of the tribe Celeuthetini (Col.), 1956; p. 66, British Museum, London.

The genus *Hypotactus* was erected for two species, *Platyacus ruralis* and *papillatus* Fst. As noted above I have referred *P. novobritannicus* var. *suturalis* Hllr. to this genus. These species are recorded only from the Bismarck Islands. Species of *Platyacus* are known only from the Solomon Islands.

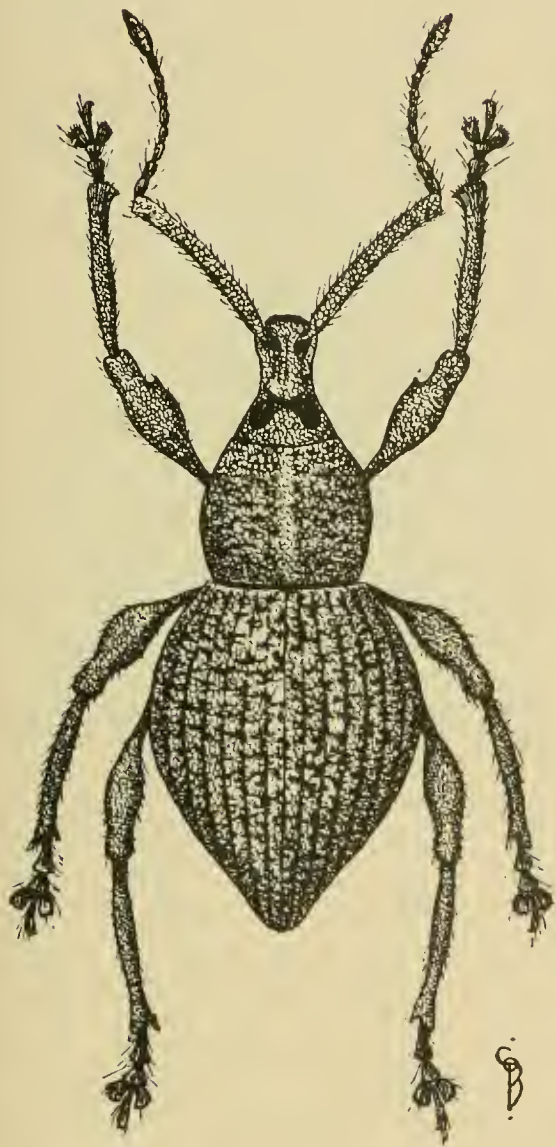


Fig. 15. *Platyacus leveri* Mshl.

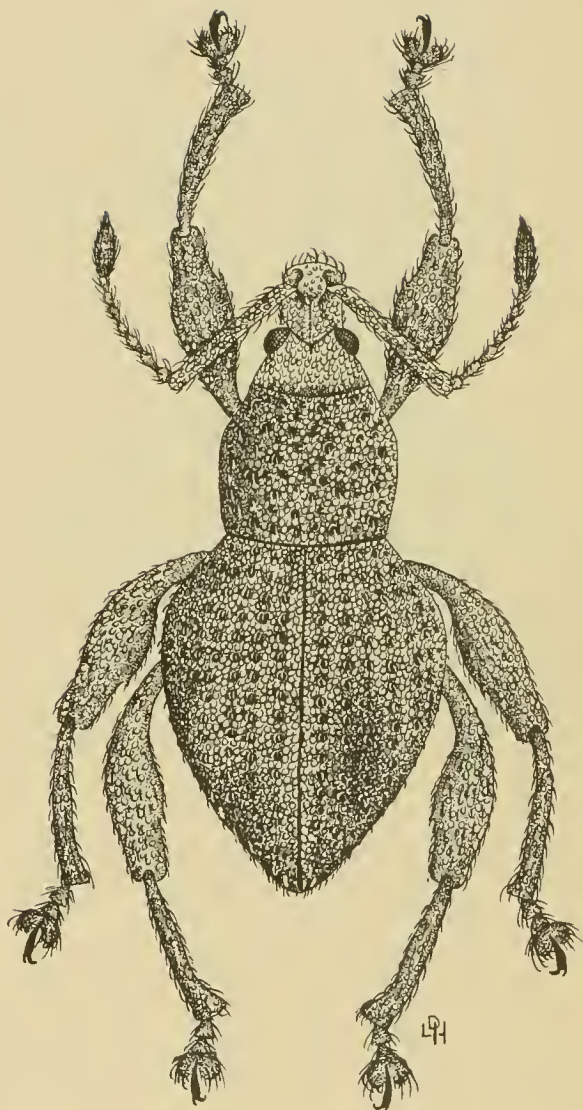


Fig. 16. *Hypotactus ruralis* Fst.

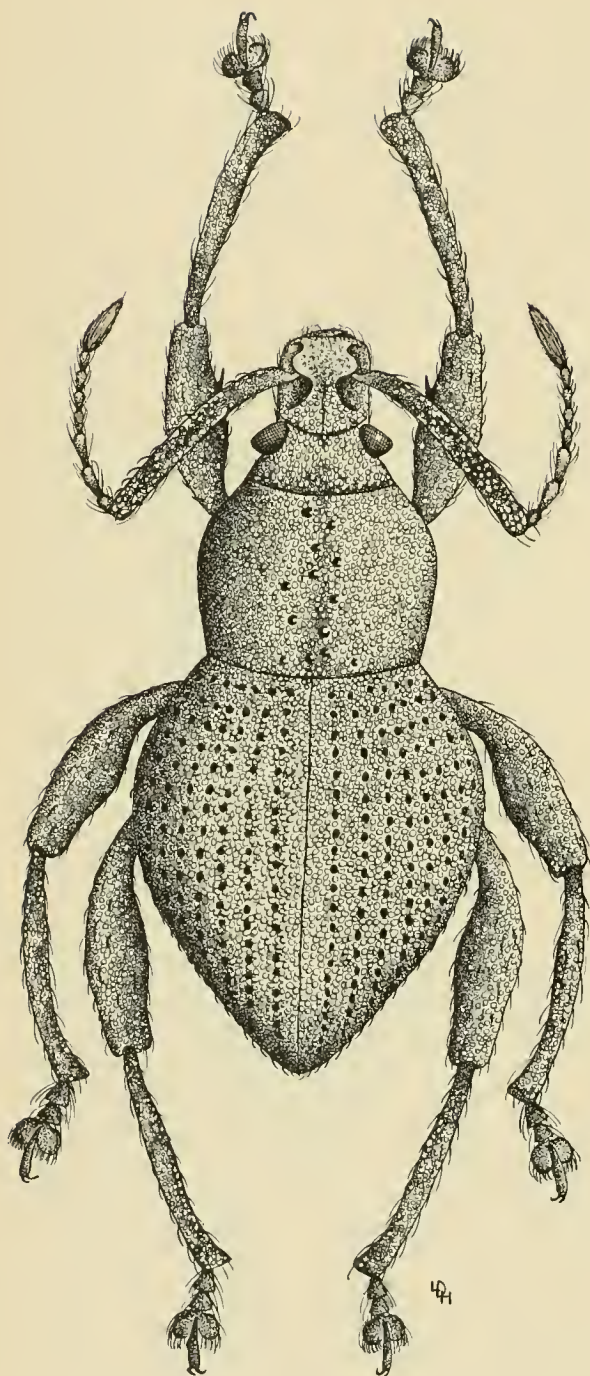


Fig. 17. *Hypotactus papillatus* Fst.

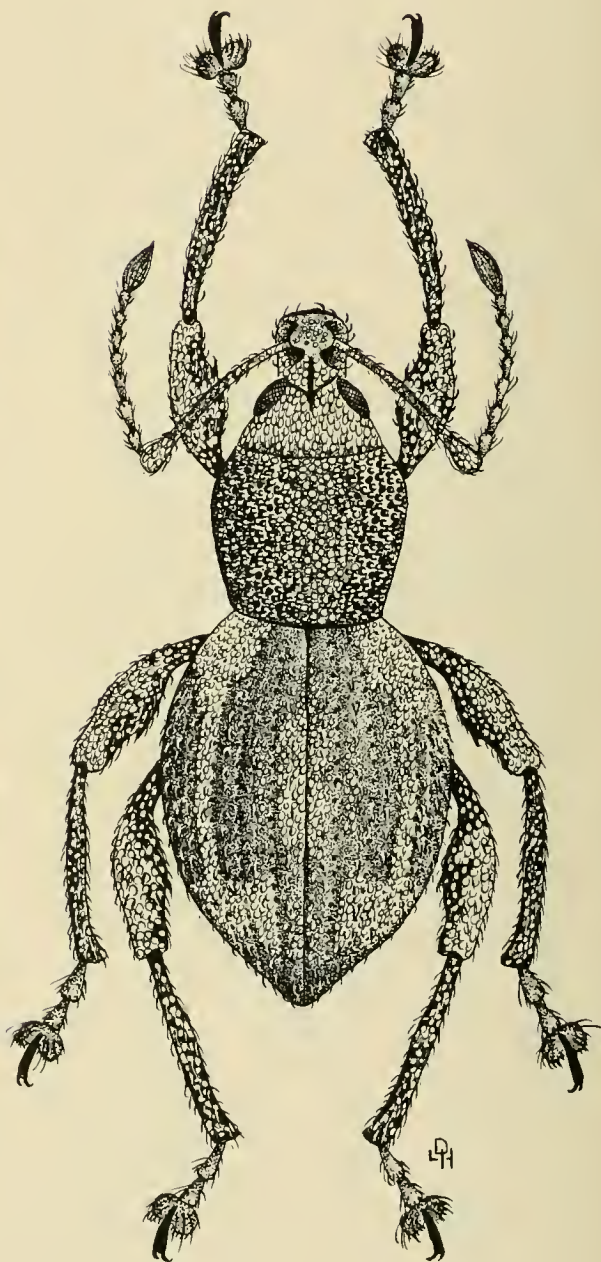
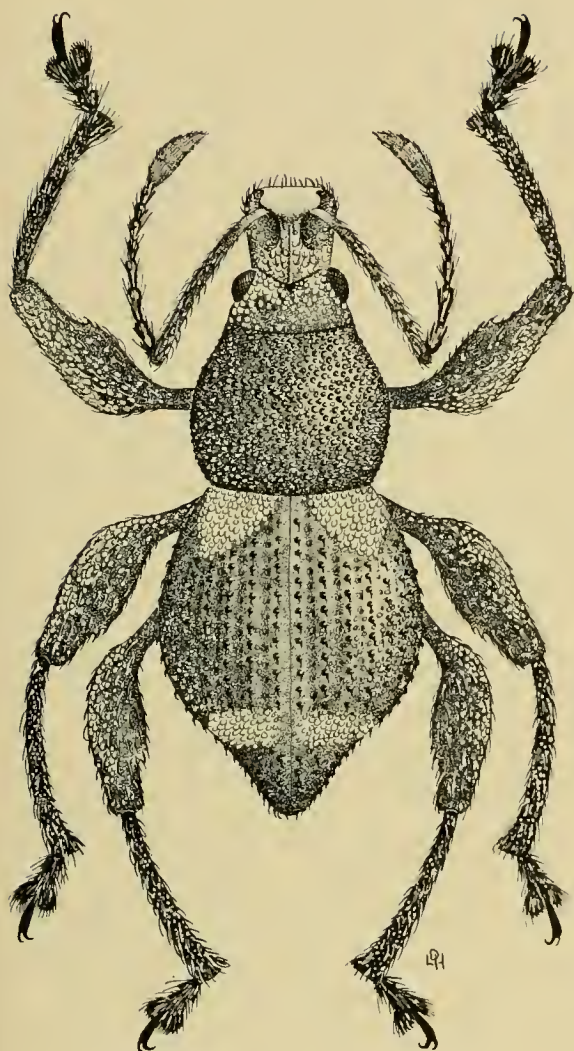


Fig. 18. *Hypotactus novobritanicus* var. *suturalis* Hllr.

Fig. 19. *Paratastus carbunculus* Hllr.

GENUS TRIGONOPS GUERIN (1841)

Guer. Rev. Zool. 1841, 10. 128.

The genus *Trigonops*, so far as now known, is confined, in the main, to the Solomon and New Hebrides Islands. It was first recognized

and described by Guérin in 1841, the genotype being *rugosa* Guérin.

The salient characteristics of the genus are: Body and prothorax globular; rostrum abruptly declivous dorsally at apex, declivity of rostrum squamose; scape similar in both sexes, not compressed, subcylindrical, very gradually widening from base to apex; funicle with joint 2 not longer than 1, eyes highest behind middle, mostly very strongly produced; elytra often granulate but without conical tubercles, with ten regular striae, but tenth often abbreviated and approaching very closely to 9, punctures comparatively large in basal third, much smaller behind, female in many species with tuft of setae on posterior declivity of elytra. Tibiae not carinate dorsally; metasternal suture, visible only near its base; femora without teeth; mesosternal process much broader than long; legs rather long with femora swollen toward extremity.

Sir Guy A. K. Marshall in his study of the tribe Celeuthetini divided the thirty-six species of the old widespread genus *Trigonops* as listed in the Coleopterorum Catalogus, pars 160, 1937, pp. 313-315, into six genera thus leaving only fifteen species as typical *Trigonops*, these he considered as confined to the Solomon Islands area. Since K. M. Heller of the Dresden Museum had described eleven of the fifteen species it was most necessary that specimens from the type series be made available for study. Through the kindness of Herrn Dr. Wilhelm Gotz, Hauptdirektor, Staatliches Museum für Tierkunde, Dresden, a loan of cotype specimens of all of the Heller species was made available. Drawings and comparisons with specimens from the assembled collections of *Trigonops* from the Solomon Islands were made. I have studied specimens of all twenty-five species included in this report, with the exception of *vitticollis* Fairm, which is unknown to me.

Since some species are rare and not in most collections, much care has been taken to provide a carefully prepared illustration of each species dealt with in this genus.

KEY TO SPECIES OF GENUS TRIGONOPS GUERIN

1. Elytra punctate with longitudinal series of strongly elevated tubercles, close to each other, forming lines or ribs between which are a series of smaller tubercles; prothorax rugose; size 5.5-6.5 mm in length-3.5-3.6 mm in width. Solomon Islands. genotype, Fig. 20 *rugosa* Guérin
- Elytra without strongly elevated tubercles, close to each other, forming lines or ribs 2

2. Humeral margin of elytra, on both sides, with an outward projecting tooth 3
- Humeral margin of elytra without an outward projecting tooth 4
3. Prothorax flattened on the disc; sides strongly rounded, wider than long. Size 5.5 mm in length—3 mm in width. Kolombangara, Western Group. Fig. 21 *planicollis* Hllr.
- Prothorax not flattened, sides moderately rounded; rugulae; wider than long. Size 5.0–6.5 mm in length—2.5–3.0 in width. New Georgia Island. Fig. 22 *paravicinii* Hllr.
- Prothorax longer than wide, reduced at apex; with large gray and greenish scales; small species, size 3.0 mm in length—1.5 mm in width. Shortland Island. Fig. 23 *minuta* n. sp.
4. Lateral margin of prothorax in basal half not angular; longer than wide, tapering from base to apex; with deep punctures; elytra with deep punctures; small iridescent scales. Size 5.0 mm in length—2.9 mm in width, Bougainville Island. Fig. 24 *irrorata* Hllr.
- Lateral margin of prothorax in basal half angular; as long as wide; coarsely and deeply punctured; lateral border with a sharp edge; scales green; elytra rotundate, punctures regular and shallow. Size 5.0 mm in length—2.5 mm in width. Bougainville Island. Fig. 25 *salomonis* Hllr.
5. Eyes blunt and conical, the vertex shifted toward the back 6
- Eyes round, less conical 8
6. Prothorax as wide as long, punctures not as large as the interspaces; elytral punctures deep, small keel on fourth interval at declivity on the ♂. Size 5.0–5.6 mm in length—2.7–2.9 mm in breadth. Russel Island. Fig. 26 *froggatti* Hllr.
- Prothorax wider than long, sparsely punctate, elytral punctures shallow; deeply emarginate at apex. Size 7.2 in length—3.5 mm in breadth. Solomon Islands. Fig. 27 *coerulescens* Blanch.
7. Prothorax wider than long; surface closely tuberculate, tips of tubercles black, shining; scales sparsely placed on the interspaces; elytra longer than wide; punctures deep with clusters of scales and small black tubercles showing through from the intervals between the punctures. Size 4.5–5.2 mm in length—2.5–2.0 mm in breadth. Santa Isabel Island. Fig. 28 *marshalli* n. sp.
8. Rostrum narrow, as long as head; sulcus deep and more crescent shaped; eyes prominent; prothorax wider than long, convex; keel on 4-5 intervals of elytra at declivity; size 6.0–7.1 mm in length—3.0–3.8 mm in breadth. Malaita Island. Fig. 29 *exophthalmus* Hllr.
- Rostrum narrow, as long as head; sulcus shallow V shaped; eyes conical; prothorax as wide as long; clothed with closely set green scales; body compact, punctures prominent and deep on elytra; keel on declivity less prominent. Size 4.5–5.2 mm in length—3.0–3.4 mm in breadth. Guadalcanal Island. Figs. 30-31 *becki* n. sp.
9. Eyes round, large, convex; rostrum wider than long; scrobes large, hollow, sulcus deep, straight, prothorax with large lateral punctures; keel extending from middle of elytra to declivity; body robust. Size 7.1–9.2 mm in length—3.5–4.2 mm in breadth. Guadalcanal Island. Figs. 32-34. *platessa* Hllr.
10. Eyes round, placed well down on side of head; antennae scape slender, scrobes open posteriorly; carina with prominent elevation at rostral declivity, declivity scaleless; prothorax surface granular, with a fine black medium carina;

elytra with small anterior elevation on intervals 2-3; and on intervals 4-5 at declivity. Derm black with small, round, brown scales. Size 4.8-8.0 mm in length-2.5-3.1 mm in breadth. Florida and Guadalcanal Islands. Fig. 35.

- *granulosa* n. sp.
- Eye round, small, slightly pointed; rostrum wider than long, scrobes prominent, sulcus crescent-like; scape slender; prothorax with distinctive scale pattern; elytra with deep punctures, small species. Size 4.0-4.3 mm in length-2.0-2.3 mm in breadth. Isabel, Florida, and Guadalcanal Islands. Fig. 36
- *isabellae* n. sp.
11. Prothorax much wider than long; median carina extending the full length of prothorax, elytra emarginate at apex; interval 9 enlarged and thickly covered by gray scales and short setae; size 8.5-8.6 mm in length-3.1-3.3 mm in breadth. Bougainville Island. Fig. 37 *carinithorax* Hllr.
- Prothorax wider than long; median carina obscure; elytra less emarginate at apex, apical enlargement of interval 9 more pronounced; scales green with distinctive pattern; size 7.8-12.3 mm in length-3.5-5.0 mm in breadth. Buka and Bougainville Island. Fig. 38 *bougainvillensis* n. sp.
12. Prothorax much wider at base than apex; wider at middle, antenna scape slender; body rotund, ventrites 1-2 with deep punctures; sparse setae and no scales 13
- Prothorax strongly emarginate at base, disc flattened; scrobes large and open, narrowly separated by the rostral carina 14
13. Body rotund, elytral apex precipitous; prothorax longer than wide, tapering from base to apex; elytral punctures deep; closely surrounded by small gray scales. Size 4.0-4.8 mm in length-2.1-2.4 mm in breadth. Guadalcanal Island. Fig. 39 *guadalcanalensis* n. sp.
- Body with elytra slightly longer than wide; apex acute; prothorax as long as wide; rostrum longer than head; scales whitish-gray; size 3.5-5.5 mm in length-2.0-3.6 mm in breadth, Kolombangara Island. Fig. 40 *helleri* n. sp.
- Body elytra similar to *helleri*; sides of prothorax almost parallel, disc flat, as wide as long, no median carina or punctures showing, evenly covered, with pearl gray scales. Size 4.0-5.0 mm in length-2.0-2.3 mm in breadth. New Georgia Island. Fig. 41 *seriatopunctata* Hllr.
14. Elytra elongate, prothorax angular at base, both flat transversely, punctures and striae obscured by gray and brown scales-size 5.0-6.8 mm in length-3.1-3.8 mm in breadth. San Cristobol Island. Fig. 42 *dilatocollis* Gunther
- Elytra ovate, short, apex obtusely acuminate; base not all latioribus; prothorax narrow longitudinally, greatly narrowed toward the apex; eyes convex, but not pointed; ventrites 1-2 connate. Size 7.0 mm in length. Duke of York Islands. Description page *vitticollis* Fairm
15. Rostrum shorter than head; sulcus crescent-shaped; two dark blotches at base of prothorax; elytra flattened, covered by blue-gray scales. Size 4.5-2.6 mm in length-2.5-2.6 mm in breadth. Specimens studied were collected on Sikaiana or Steward Coral Island; about 110 miles east of Malaita Island. Type locality; Nukumanu, an atoll about 250 miles ENE of Bougainville, sometimes called Tasman Island. Fig. 43 *notaticollis* Hllr.
- Rostrum as long as wide; sulcus straight, a V-shaped fovea at head junction with sulcus; Prothorax wider than long, dorsally flattened; constructed near apex; puncture with small, black tubercles showing through scales, elytra are evenly and fairly deeply punctate; covered with bluish-green scales. Size 7.0-

7.2 mm in length—3.2–3.5 mm in width; Russel and Guadalcanal Islands. Fig. 44 *forticornis* Hllr.

16. Prothorax with deep angular punctures, rostrum longer than wide; base tumid, sulcus deep, wide and straight, elytra with deep punctures, size 4.8–6.1 mm in length—2.6–3.6 in breadth. Bougainville Island. Fig. 45 *gressitti* n. sp.

— Prothorax without deep angular punctures; rostrum much longer than wide, antennae scape slender and curved; scales greenish blue, forming a distinctive pattern, a small species; size 3.1–3.2 in length—1.4–1.5 mm in breadth. Bougainville Island. Fig. 46 *gloriosa* n. sp.

Trigonops rugosa Guérin

Guérin-Meneville. Rv. Zool., 1841, p. 128.

Fig. 20

Derm dull black with small blue scales on rostrum, head, prothorax, elytra, legs, and under side of body, decumbent setae sparse.

Rostrum as long as head, with a conic elevation on its superior extremity. Scrobes deep and wide, separated by conic elevation, rostrum separated from the head by a curved sulcus. *Head* short, wider than long, eyes situated well down on side of head, in the form of two cones, with points directed slightly toward rear. *Antennae* rather slender, scape reaching middle of prothorax, gradually expanding toward apex, funicle as long as scape, segments 1-2 longer than 3-4-5 combined, club as long as segments 5-7 combined. *Prothorax* wider than long, convex, widest just back of middle, slightly constricted near apex, base and apex truncate, disc rugose, with few small blue scales. *Elytra* much wider than prothorax, almost as wide as long, globular, a little attenuated at apex, disc with longitudinal series of elevated tubercles, close to each other and forming ribs or rows between a series of smaller tubercles; declivity and lateral areas with short white setae; stria 10 complete with small punctures. *Legs*, hind femora not reaching apex of elytra, club of femora moderate in size, blue scales short setae on femora and tibia, coxae separated, ventrites 1-2 with few scales and setae, ventrite 5 as wide as 3-4 combined; 5 with long straight setae on distal margin.

Length 5.1 mm; breadth 2.9 mm.

Type locality: Solomon Islands. This species is the genotype of *Trigonops*. The genus was established on one species from the Solomon Islands, collected by members of the expedition to the South Pole, 1841.

In this study I have seen just two specimens. Sir Guy Marshall furnished one specimen labeled *Solomon Pacific Islands*. The illustration, Fig. 20,

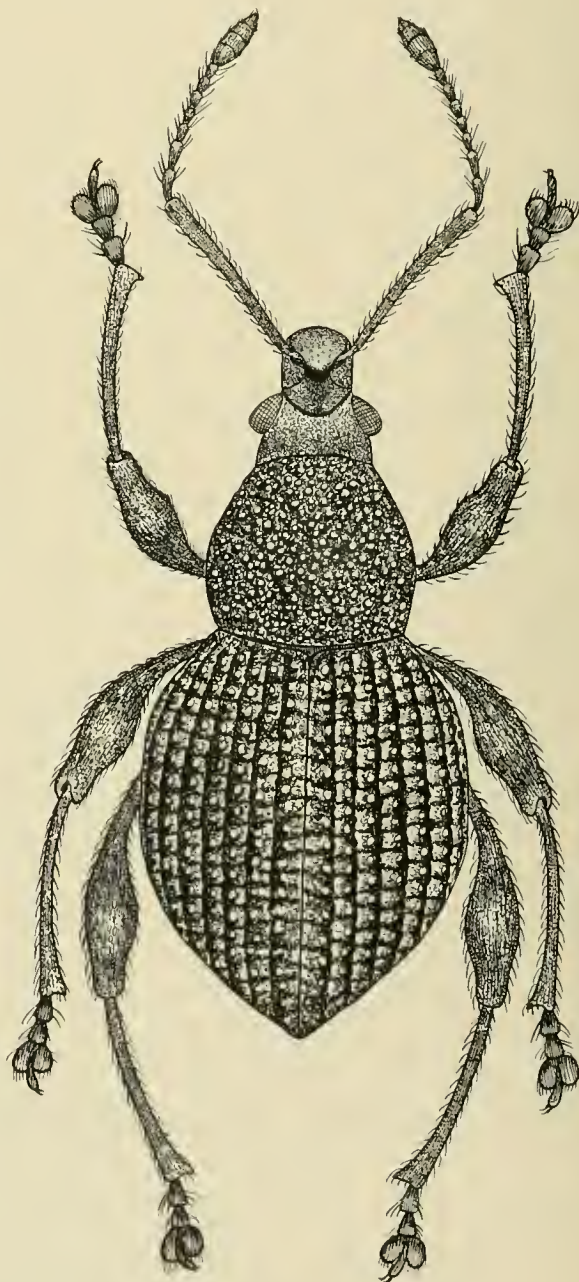


Fig. 20. *Trigonops rugosa* Guérin

was made from this specimen. It was returned to the Natural History Museum in London. One specimen is now in the Brigham Young University Entomological Collection. The right prothoracic leg, the tibia, and tarsus of the mesothoracic and the left metathoracic leg are missing, otherwise it is a perfect specimen. It bears a label *Solomon Islands*. There have been no other specimens of this species come to my attention during this study of hundreds of specimens of *Trigonops* from most of the islands of the Solomon Group.

The prominent round, rostral elevation, small, blue scales, rugosity of the prothorax and elytra, and small size are distinctive characters of *rugosa*.

Trigonops planicollis Heller

Heller, Verh. Naturf. Ges. Basel XLX, 1934, p. 16, 21.

Fig. 21

Derm rubescent, scales green and iridescent. Head small, rostrum as long as head. Vertex rugose with few blue, some green, and iridescent scales; rostral carina fine, ending in small elevation on gently sloping declivity, declivity red-

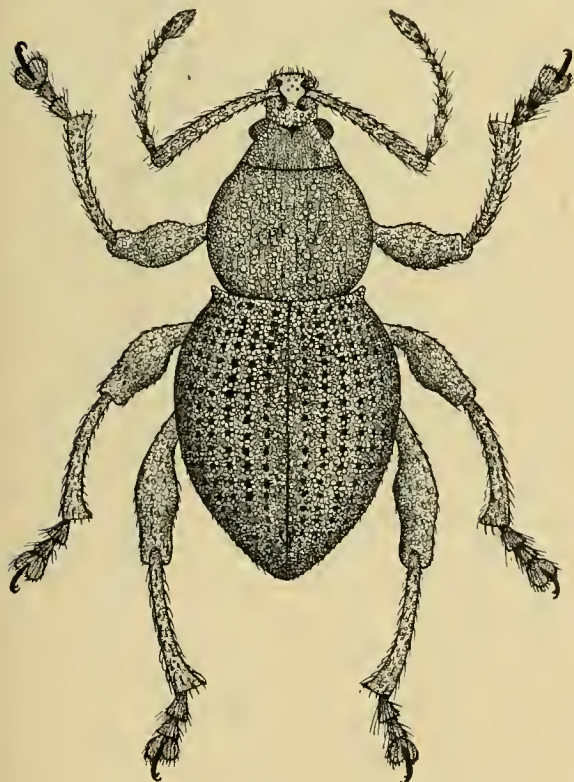


Fig. 21. *Trigonops planicollis* Hllr.

dish, practically devoid of scales and setae; serobes small, antennae scape slightly larger at apex than at base, reaching to middle of prothorax. Densely covered with black, curved setae and iridescent scales; segments 1-3 of funicle elongate; 4-7 rotundate, club small, as long as segments 5-7; segments with black setae; eyes large, rather flat and placed well down on side of head, sulcus shallow, a row of scales between eyes and sulcus. Prothorax wider than long; widest near middle, flat transversely, scales roundish and more dense on lateral margins, no median carina, punctures small and close, apex and trunk truncate. Elytra one-fourth longer than broad, broadest near base, base slightly concave; humeral spine near base of striae 8-9, disc convex transversely; striae with deep punctures, scales on intervals of declivity in female; ten regular striae, somewhat emarginate near apex which is rather acuminate. Legs reddish with hind femora extending beyond apex of elytra, bulbous part three times width of base; dorsal surface of femora and tibia covered with green scales, lateral and ventral surfaces with light-colored setae; anterior and middle tibia bowed. Venter and ventrites sparsely covered with scales, punctures deep, but widely separated, ventrites 3-5 devoid of scales and setae.

Length 5.5 mm; breadth 3.0 mm.

Type locality: Solomon Islands, July 1909 (W. W. Froggatt).

Distribution of specimens studied: Solomon Islands, Western Group, Kolombangara, Kuli, October 2, 1954 (E. S. Brown); Arundel Isl., Nauru, ♂ and ♀, August 6, 1936 (R. A. Lever); Rendova, May 1957, (R. G. Fenimore). Collected on cocoa foliage.

The specimens collected by Lever and Fenimore agreed with the cotype specimen loaned to the author by Herrn Dr. Gotz of the Museum für Tierkunde, Dresden.

Heller in commenting on *planicollis* said it is in the stature, on the average, a little smaller, the tooth on both sides of the elytral humerus, smaller and blunter, the prothorax wider; elytra uniform; punctures covered with green scales, femora extending beyond the tip of the elytra in contrast to *paravicinii*.

Trigonops paravicinii Heller

K. M. Heller, Verh. Naturf. Ges. Basel XLV, 1934, p. 16.

Fig. 22

Derm black, except the legs and rostrum which are reddish in color.

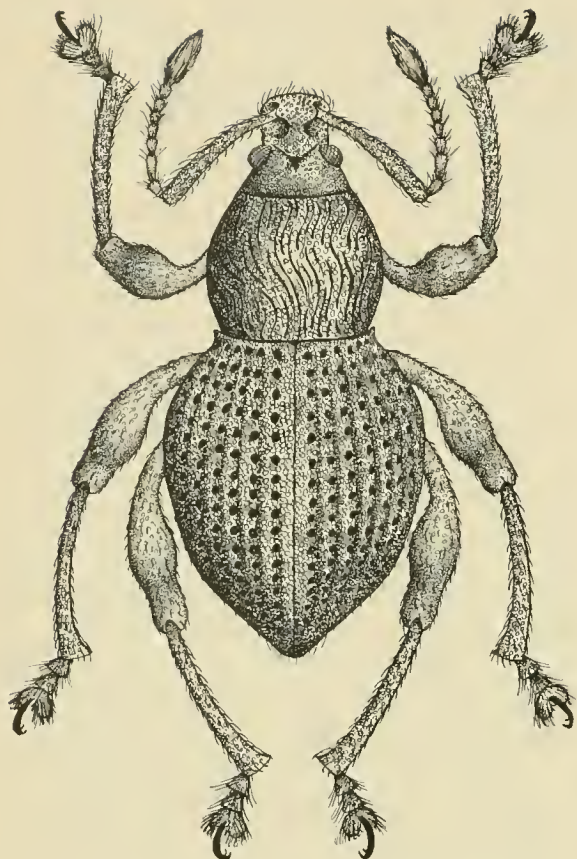


Fig. 22. *Trigonops paravicinii* Hllr.

Head shorter than rostrum rostral sulcus V-shaped; carina fine, distinct and black, blending into declivity without an elevation; eyes placed well down on side of head, flattened, vertex mildly rugose with small blue and greenish scales, widely separated; scape of antennae large gradually expanding in diameter towards apex, segments 1-2 of funicle elongate, others cylindrical, club longer than segments 5-7. Prothorax truncate at apex and base, width at middle 2.2 mm; length 2.1 mm, disc slightly convex with longitudinal wavy ridges, punctures in intervals, small blue-green scales on costae. Elytra oval, widest near base, convex transversely, deep punctures in striae, intervals with small, bluish scales, some larger scales scattered around punctures; declivity precipitous, lateral humeral area of elytra with small, sharp tooth. Legs reddish in color; femora club enlarged near apex, not reaching tip of elytra, femora and tibia with small, green scales, ventrites 1-2 laterally sparsely clad with small scales, punctures few and shallow with decumbent setae; 3-5 ventrites devoid of scales.

Length 6.9 mm; breadth 3.8 mm.

Type locality: New Georgia, Ratuna; July 1932.

Two cotype specimens, a male and a female, from the Heller Collection in the Museum für Tierkunde, Dresden, were compared with a specimen from Sir Guy Marshall, which he had compared with a cotype female specimen. These three specimens are from the type locality.

This rare species is characterized by the reddish legs and rostrum, prothorax slightly convex with longitudinal wavy ridges, lateral humeral area of elytra with a small, sharp tooth, and body clothed with small blue-greenish scales.

Trigonops minuta n. sp.

Fig. 23

Derm black, with pale green scales in longitudinal pattern, prothorax with a narrow median line devoid of scales, showing well-developed punctures.

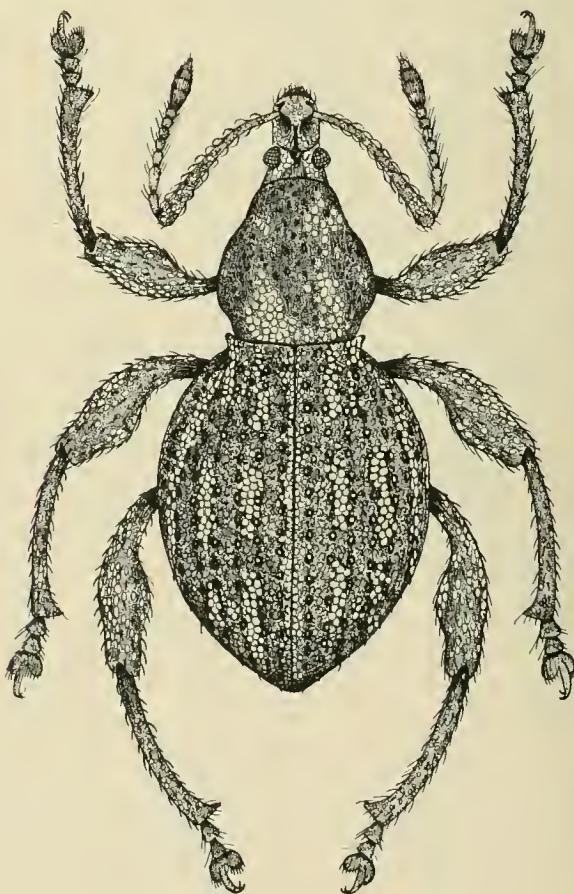


Fig. 23. *Trigonops minuta* n. sp.

Head and rostrum as long as prothorax, separated from rostrum by a curved carina slightly elevated and acute at junction of apical declivity sparsely covered with small, pale green scales. *Antennae* with scape densely squamose with decumbent setae which appear in circular rows; scape widening from proximal to distal end; funicle segments 1 and 2 longer than combined length of segments 3-5; club stoutly oval, as long as three preceding funicular segments; scrobes large, open dorsally. Eyes rather large, round, in contact with lateral rostral sulcus. *Prothorax* wider than long, broadest just back of middle; apex narrower than base; slightly constricted near apex; disc flattish, densely and rather coarsely punctured, scales same size as those on elytra. *Elytra* two-fifths of millimeter longer than wide, widest at middle, base slightly concave, humeral angle with prominent spine; disc convex with prominent interstrial punctures covered by pale green scales in irregular patterns, except a row of uniform scales along elytral suture; sparse decumbent white setae along lateral and declivitous portion of elytra; stria 10 approaching very closely to 9. *Legs*, with hind femora reaching to apex of elytra; densely covered with pale green scales; sternum, prosternum, and mesosternum densely covered with pale green scales, punctures and white decumbent setae. First and second ventrites covered laterally with pale green scales, 3-5 devoid of scales, fifth ventrite large with decumbent setae.

Length 3 mm; breadth 1.8 mm.

Type locality: Solomon Islands: Holotype, Shortland Island, Lofung, 9-X-1936; Collector R. A. Lever. Holotype and one paratype from Shortland Island, same data as holotype, also one paratype 659, Choiseul Island, Luti I-VIII, 1958, Collected by F. G. Fenimore, C. L. E. Coll. No. 16234, and one paratype Fauro Island, 89.3 all deposited in the British Museum of Natural History, London. Two paratypes deposited in Entomological Collection, Brigham Young University, 1-659 Choiseul Island, Luti, 1-VIII, 1958, Coll. F. G. Fenimore, and 1 Ysabel Island, March, 1932, Coll. R. A. Lever. One paratype Bougainville Island (S), Kokure, Nr. Crown Prince Rd. 900 m. June 11, 1956, deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii (E. J. Ford, Jr.).

Remarks: The small size, humeral tooth, curved setae on scape and round, rather large eyes for a small species, serves to distinguish it from other *Trigonops* species of this study.

Trigonops irrorata Heller

K. M. Heller, Verh. Naturf. Ges. Basel XLV 1934, p. 20, 21, T. 1, Fig. 14

Fig. 24

Derm black, with iridescent, roundish scales. *Head*, rostrum narrow, but longer than head, sulcus falciform and deep extending laterally to scrobes, rostral carina narrow and prominent, declivity with small scales and erect setae. *Antennae* scape gradually widening from origin to apex, extending to middle of prothorax, segments 1-4 of funicle long, 5-7 shorter. *Eyes* rather flat, extending down on to rostrum similarly to that of *T. solomonis*. Club large as long as segments 5-7; setae on scape and segments black and bent in a circular shape. *Prothorax* narrow gradually widening from apex to base; apex slightly emarginate, base truncate, slightly widest at middle; with deep punctures on rather flat disc, median area without scales, an area of scales between median line and lateral margin; lateral margin without scales. *Elytra* with deep punctures, intervals narrow, scale pattern cross-wise except on median suture and at base; oval in shape, con-

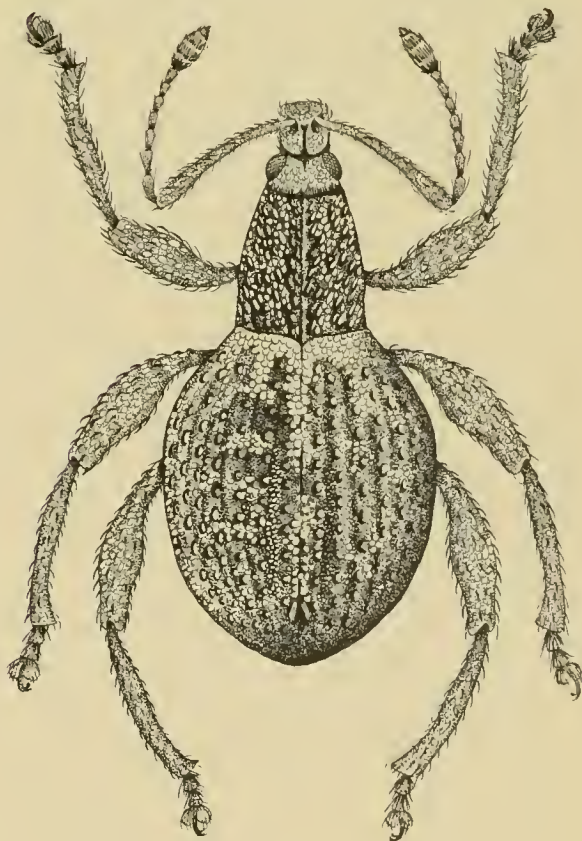


Fig. 24. *Trigonops irrorata* Hllr.

vex transversely; with tuft of setae on declivity. *Legs* black, femora swollen at posterior third, not reaching apex of elytra.

Length 4.5-5 mm; breadth 2.7-2.9 mm.

Type locality: Solomon Islands, Bougainville, 1930-2 (Dr. Staudinger and Haas).

T. irrorata is known to me, only through the kindness of Herrn Dr. Wilhelm Gotz of Dresden, who loaned me a single cotype specimen. The above description and Fig. 24 are based on it. I have examined hundreds of specimens of *Trigonops* from the Solomon Islands, but have not found a specimen of this species. All the cotype specimens of *Trigonops* were returned to the Dresden Museum.

The falciform rostral sulcus, rather flat eyes, narrow elongate prothorax and globose elytra serves to distinguish *irrorata* from other species of *Trigonops* thus far studied.

Trigonops solomonis Heller

Heller, Verh. Naturf. Ges. Basel XLV, 1934, p. 19

Fig. 25

Derm black with covering of greenish and blue scales. *Head* with long rostrum, carina fine and prominent closely covered with scales; scape of antennae bowed, enlarged at apex, not reaching middle of prothorax, funicular segments slender, segments 1-2 long, 4-5 one and one-half times as long as thick; *eyes* prominent and well down on side of head, apex pointing backwards, vertex of head with few small punctures, scales well separated. *Prothorax* longer than wide; greatest breadth near middle, surface of disc deeply punctured, lateral margins forming a sharp edge; mid-strip black, thickly punctured, apex concave at middle, width within one-tenth of elytra length giving elytra a globose appearance; elytra widest one third distance from base; slightly convex transversely; striae deep, punctures surrounded with a circle of small, greenish scales; intervals double width of striae; slight emargination near apex, female with tuft of setae on declivity. *Legs* prothoracic femora with club enlargement extending to apex; metathoracic femora not extending to apex of elytra, club poorly developed, ventrites stout, thick and marked with needle-like scratches, these segments somewhat concave in male.

Length 5.9 mm; breadth 2.9 mm.

Type locality: Solomon Islands, Bougainville Is. 1908 (Kurtz). This description and drawing was made from a cotype specimen from Staatlichen Museum für Tierkunde in Dresden, loaned

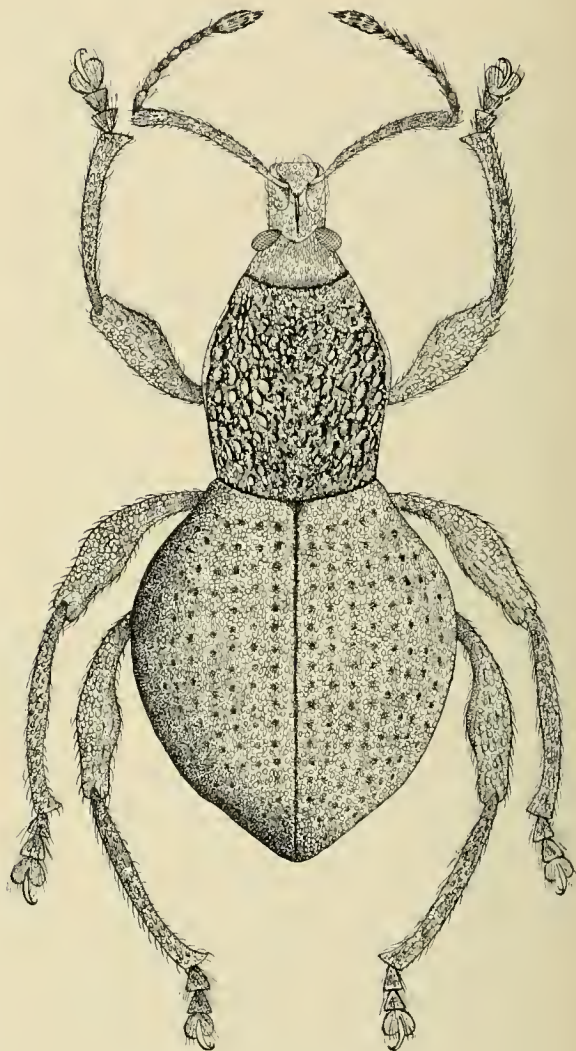


Fig. 25. *Trigonops solomonis* Hllr.

to the writer by Herrn Dr. Wilhelm Gotz, Hauptdirektor of the Museum.

Remarks: Heller points out that when *solomonis* and *froggatti* are compared with *forticornis* and *exophthalmus*, they vary sufficiently to be separated as a subgenus in the *T. rugosa* group. Lack of specimens precluded his making such a separation. *T. solomonis* is a distinctive species because of its rounded shape, size, lack of rostral hump, femoral club, and rugose prothorax.

Trigonops froggatti Heller

Heller, Wein. Ent. Zeit. XXIX, 1910, p. 189. Fig. 4

Fig. 26

Derm black, covered with green scales except on the prothorax where there are some scattered iridescent ones.

Rostrum longer than wide, separated from head by a V-shaped sulcus; carina as wide as distal end of scape, not elevated at rostral declivity which bears a few small green scales. *Antennae* scape bowed, becoming enlarged at distal end, scape short, extending only to anterior third of prothorax; segments 1-2 of funicle equal in length, and as long as segments 3-6 combined, club as long as segments 5-7; scales on scape black, setae on funicle. *Head* shorter than rostrum, eyes placed well on side of head, frons with small granules and a mixture of green-blue scales. *Prothorax* as wide as long, widest at middle constricted near apex; greatly sloping to base, apex and base truncate, strongly convex, with median line of small tubercles devoid of scales; covered mainly with green scales, intermixed with scattered iridescent and blue scales, punctures obscured by scales. *Elytra* about three-fourths as broad as long; base slightly concave, broadest before middle, rather evenly rounded laterally behind middle, pointedly narrowed to apex, disc convex; striae deep and distinct, each puncture surrounded by a rosette of scales, intervals 3-4 slightly elevated caudad. *Legs*, hind femora extending slightly beyond apex of elytra, densely squamose, setae obscure, club about three-fourths of distance from base

to apex and twice as broad as base, all legs black in color. Undersurface covered with green scales, except center portion of ventrites 1-2; 4-5, with setae sparse, white and decumbent.

Length 5.2-6.1 mm; breadth 2.9-3.1 mm.

Type locality: Solomon Islands, Russell Island, (W. W. Froggatt), July-August 1909.

Distribution of specimens of this study: Florida Islands: April 14, 1944 (Harry P. Chandler), September 1932 (R. A. Lever); Tulagi Island: January to October 1932 (R. A. Lever), April 22, 23, 1922 (E. A. Armytage), August 12, 1933 (H. T. Pagden); Guadalcanal Island: June 24, 1954, Reva Vatu (E. S. Brown), June 21, 1954; Kua Vatu (E. S. Brown), July 15, 1944, Tenasu River Area (D E. Beck); August 3, 1957 (P. T. Fenemore).

D E. Beck collected this species on a dead log near the Kulinigrass Area, R. A. Lever found it on hibiscus leaves, and H. T. Pagden reports it from coconut.

Heller points out that *froggatti* may be confused with *coerulescens* Blanch.

From the results of this study these two species are found to be quite different. In *froggatti* the rostral suture, and base of the rostrum are more angular and tumid; the prothoracic femora are shorter and more robust, the prothorax is widest at about the middle and with deeper punctures, and the elytra are less parallel and more apically pointed than in *coerulescens*.

Trigonops coerulescens Blanch

Blanchard, Voy. Pole Sud. IV, 1853, p. 232, Fig. 5

Fig. 27

Dern black, body completely covered with light blue scales.

Rostrum short, as long as head, heavy set, declivity at apex wide with small blue scales, long white setae laterally, conical elevation at apex of carina, basal area with blue scales and white setae, separated from head by a curved V-shaped sulcus. *Antennae* large, scape reaching to middle of prothorax, rotund, same diameter throughout, covered with blue scales and low lying white setae; funicle segments 1-2-3 elongate oval, segments 4-7 shorter and smaller, club downy, slender, as long as segments 5-7 combined, segments with long gray setae. *Head* convex, scaly, lightly striated in middle, punctures few and small; eyes large, not strongly convex, slightly inclined posteriorly. *Prothorax* with greater breadth than length, widest at middle, base and apex truncate; slightly constricted

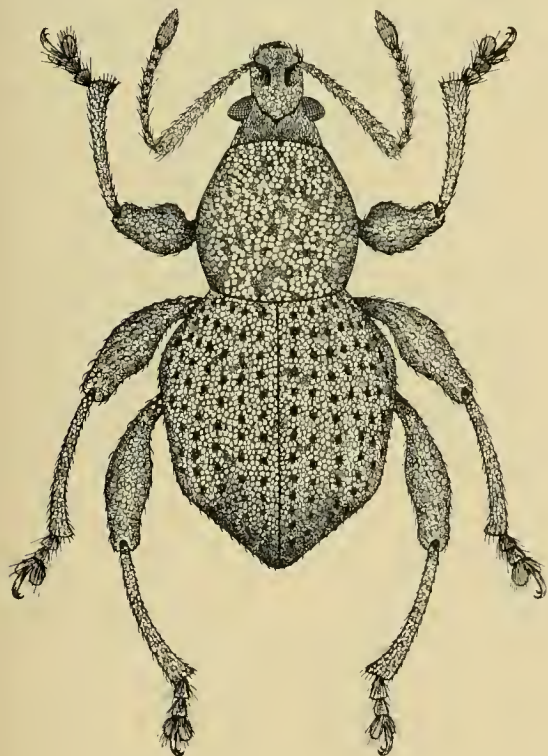


Fig. 26. *Trigonops froggatti* Hllr.

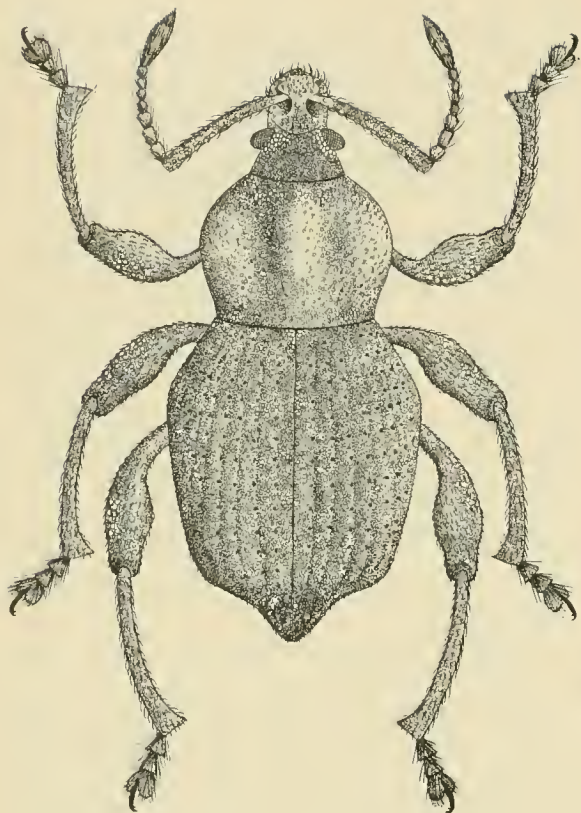


Fig. 27. *Trigonops coeruleus* Blanch.

near apex, lateral margins elevated; center of disc flat, with slight elevation toward apex; surface rough due to small tubercles and punctures; stripes of blue scales border the median area. *Elytra* widest near base; tapering to a slender apex; elevated near declivity along 5-6 striae, central part of disc flat or slightly cupped; punctures deep covered with scales, intervals prominent, declivity abrupt. *Legs*, femora clubs large, scales sparse, color reddish-brown, not reaching end of elytra, underside of body with blue scales, except ventrites 3-5; ventrite 5 with white setae. Length 7.8 mm; breadth 4.1 mm.

Type locality: Solomon Islands: Saint George Island, 1941 (H. Gúerin). Specimens available for this study: Guadalcanal Island: -3 specimens from Wanderers Bay (Woodford). Two specimens in the British Museum of Natural History, London, England. One specimen in the Brigham Young University Entomological Collection.

T. coeruleus may be readily recognized due to the following characteristics: the conical elevation at apex of rostral carina; wide prothorax; elytra with lateral elevations and cupped center, abrupt apical emargination, and its size. This species resembles *carinithorax* in the shape of the prothorax and elytra. The eyes, sulcus of

rostrum, antennae, scale color and shape are different.

Trigonops marshalli n. sp.

Fig. 28

Body derm black, clothed blue and green scales.

Rostrum as broad as long, as long as head, carina short, narrow, and tumid at base, with a small elevation at declivity which bears a few small scales; sulcus crescent-shaped with a fovea at apex of head; scrobes deep and open. *Antennae* scape slender, enlarged a little at apex, segments 1-3 of funicle elongate and equal, segments 4-7 obpyriform, club as long as 5-7 combined. *Head* punctate with waved lines converging on apical fovea, and with small scales. *Eyes*

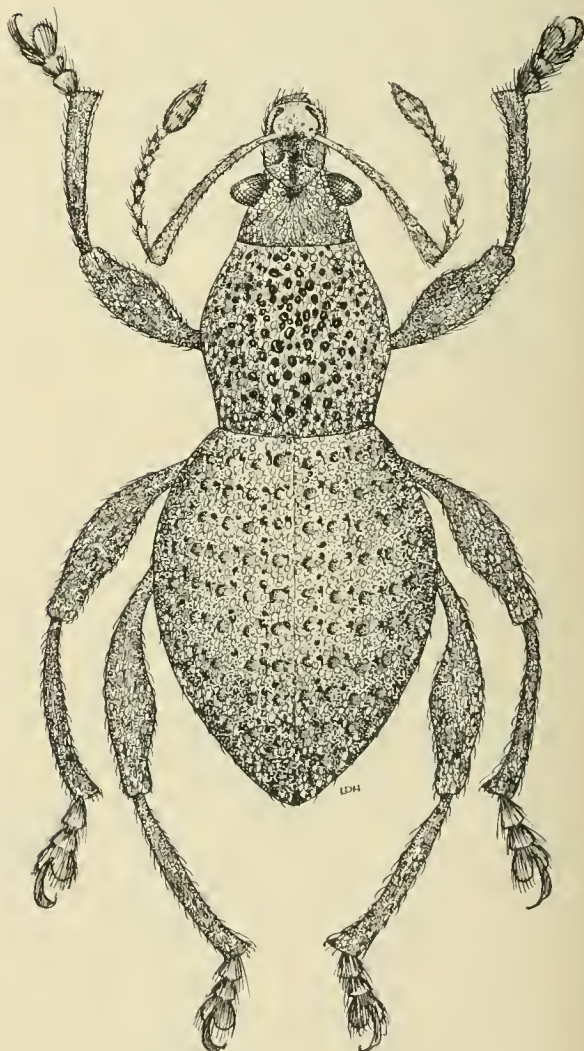


Fig. 28. *Trigonops marshalli* n. sp.

pominent, conical, tapering part directed backward. *Prothorax* wider than long, greatest width at middle, base and apex truncate; constricted slightly near apex; convex transversely; surface closely tuberculate, tips of tubercles black, shining; scales sparsely placed on interspaces. *Elytra* ovate, longer than wide, greatest width at middle, punctures deep with cluster of scales and small, black tubercles showing through from intervals between punctures; lateral emargination at apex of elytra; femora, tibia and tarsus with blue or green scales; ventrites 1-2 covered laterally with scales, 3-5 scaleless, with small setae.

Length 4.5-5.2 mm; breadth 2.5-3.0 mm.

Type locality: Solomon Islands; Holotype, Santa Isabel Island, B. S. I., Soasokera, X-19-1960(J. Tuhua); Allotype, Santa Isabel, II-1933 (R. A. Lever); 11 Paratypes, Santa Isabel Island.

Allotype and three paratypes deposited in the Entomological collections of the British Museum of Natural History, London. Holotype and three paratypes deposited in the Entomological Type collection of Brigham Young University, Provo, Utah; paratypes deposited in the Bishop Museum, Honolulu; U. S. Natural Museum, Washington, D. C., and California Academy of Science, San Francisco.

T. marshalli is a distinctive, handsome species. The color of the scales, scape of antenna slender, prominent elevation on the rostral carina, wavy lines on the vertex of head, shining tubercles on the prothorax and elytra, ovate shape of the abdomen and size characterize this species.

I am pleased to dedicate this species to the memory of Sir Guy Marshall, distinguished authority and student of the Circulionidae, and as an expression of my appreciation for his cooperation and suggestions at the inception of this project.

Trigonops exophthalmus Heller

Heller, Wien Ent. Zeit. XXIX, 1910, p. 187.

Fig. 29

Derm black with small blue-green and or white scales, rostral suture curved and slightly V-shaped, prothorax globose. Rostrum one and one-half times as long as wide, sides parallel, basal union of rostrum with head tumid and circular, carina slightly elevated at narrow area between scrobes, small scales on rostral declivity. *Antennae* scape bowed, enlarging toward apex, extending gradually to

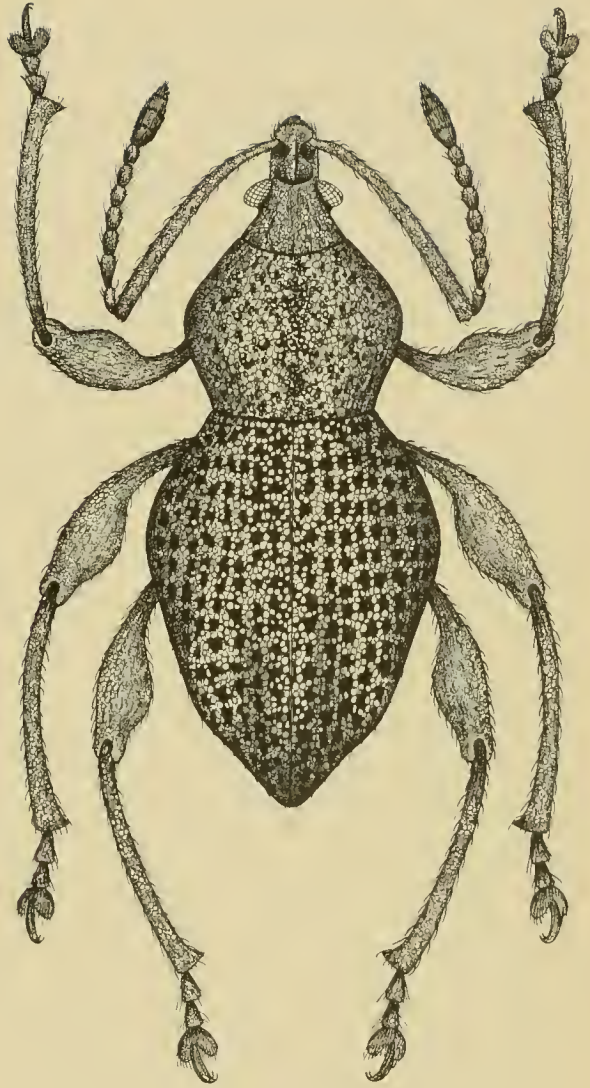


Fig. 29. *Trigonops exophthalmus* Hllr.

middle of prothorax, segments 1 and 2 of funicle slender and equal in length, club longer than three preceding ones. *Head* slightly convex, frons heavily scaled with small scales between rugose surface and small granules; eyes prominent, their crowns receding and rounded. *Prothorax* globose, widest before middle, retracted near apex, wider than long, small, black granules showing through scales, short median carina, punctures obscured; base and apex truncate. *Elytra* widest just before middle, three-fifths as wide as long, elevated on 4-5 striae, flat along elytral suture in males, punctures deep and prominent, scales around punctures and along intervals, apex pointed. *Legs* reddish, femora club bear except dorsal surface covered with scales and white setae, femora not reaching apex

of elytra, under surface sparsely clad with scales. Ventrites 1-2 bare except on margins, 3-5 with small, blue and white setae.

Length 7-8 mm; breadth 3-4.2 mm.

Type locality: Solomon Islands: Russell Island (W. W. Fraggatt) VII-VIII, 1909. Distribution of specimens studied: Malaita Is., Kuala district, Oct. 19, 1957 (P. C. Fenemore); Su'u-Baunani, May 1933 (R. A. Lever); Russel Is., Hui 1. Feb. 18, 1934 (R. A. Lever), Tulagi Is., May 28, 1922 (E. A. Armytage); Malaita, Tang-talau 150-200 m. Sept. 25, 1957 (J. L. Gressitt).

T. exophthalmus is characterized by a basal union of rostrum with head tumid, and circular; eyes prominent, their apices rounded and projected backward; club of antennae elongate, segments slender and short; prothorax globose and proximal portion of hind femora long and slender.

Trigonops becki n. sp.

Fig. 30-31

Derm black, with roundish scales, elevated in the center, green in the main, with a few blue and iridescent ones interspersed on the head, rostrum, scape, prothorax, ventrites, except segments 3-5 which are devoid of scales.

Head twice as wide at base as apex, eyes prominent. Rostrum longer than broad, parallel-sided, with a median area extending from V-shaped union with head to apical declivity, sparsely covered with small green and blue scales. Median scrobal area separated from the declivity by a slight elevation. Scrobes large. Antennae scape almost as broad at base as at apex, reaching middle of prothorax, with decumbent black and light-colored setae, green and bluish scale; funicle segments 1-2 as long as segments 3-5 combined, segment 1 thicker than 2, club rather stoutly oval, shorter than preceding three funicular segments. Prothorax slightly broader than long, gently rounded laterally, widest a little beyond middle, dorsum convex longitudinally, sparsely convexed with scales along middle, punctures distinct, surrounded by cluster of scales, each puncture with small decumbent setae. Elytra ovate, acuminate behind in male, more so in female, slightly emarginate at base. Three-fourths as broad as long; more than one-third wider than prothorax, broadest before middle, 10 striae well developed, punctures large, deep, densely surrounded by scales on interspaces, and especially area along elytral suture, tuft of setae on declivity of female, fourth and fifth striae distinctly elevated and carinate,

before declivity in male, sparse light setae on apical area of elytra. Legs with hind femora reaching to slightly beyond apex of elytra, femora and tibiae densely covered dorsally with small, green scales, ventral surface of tibiae scaleless, but with light setae in male. Femora in female reaching fifth ventrite, femora in both sexes bulbous, proximal portion of hind femora twice as long as bulbous area. Exposed portion of legs brownish. Trochanter, prosternum, mesosternum, and metasternum covered with green scales; middle of ventrites 1 and 2 sparsely covered with scales, scattered short seta issuing from each puncture, in some males these ventrites rather rugose. Female genitalia elongate, small, more or less membranous structure. When fully extended it is as long as the total length of the five ventrites. The styli are at the apex of the coxites and terminated by a long setae; the genital structure similar to that found in species of *Pantomorus*.

Named in honor of Captain D Elden Beck who devoted much of his time and energy in

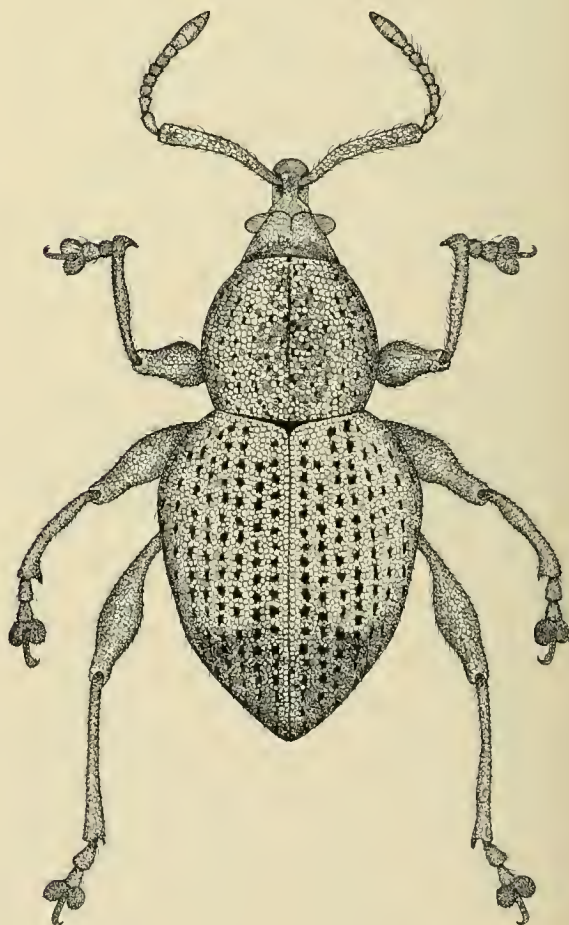


Fig. 30. *Trigonops becki* n. sp.

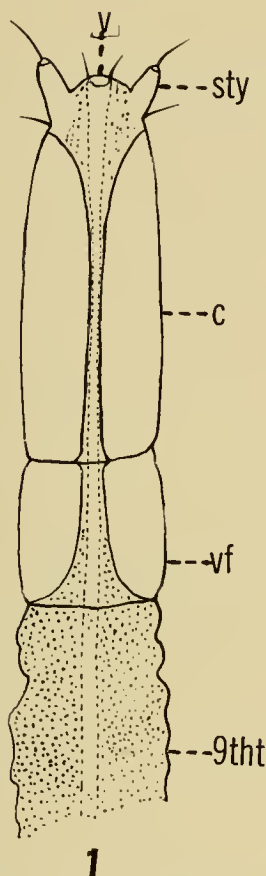


Fig. 31. *Trigonops becki* n.sp. - ♀ genitalia.

collecting and sending a representative collection of insects and reptiles from Guadalcanal Island to his Alma Mater, the Brigham Young University.

Type locality: Solomon Islands: Holotype: ♀ Guadalcanal Island, Tenura River Area, 1944 (D Elden Beck); Allotype ♂ same data as holotype; paratypes: 19 ♀ ♀, Guadalcanal, Teneru River, Henderson Field Area, 1944-45 (D Elden Beck, E. Ramey, J. Johnson); 8 ♂ ♂, Guadalcanal Teneru River Area, 1944-45 (D Elden Beck, Ernest Reinschüssel); 1 ♀ Guadalcanal, May 1, 1922 (E. A. Armytage); 3 ♀ ♀ Teneru River Area, June 16 and December 16, 1957; 3 ♀ ♀ Honiara District, Kukum, December 15, 1957 (P. G. Fenemore); 2 ♀ ♀ Guadalcanal Tunga River Bridge, August 23, 1960 (Jan Schenk); 1 ♀ Guadalcanal, Kua Vara, June 21, 1954 (E. R. Brown); 1 ♂ Malaita, su-u Baunani, April, 1933 (R. A. Lever). The type specimens and some paratypes are in the Brigham Young University Entomological Type Collection. Paratype specimens have been deposited in the British Museum of Natural History, London; the United

States National Museum, Entomological Collection; the California Academy of Sciences, Entomological Collection; and the Entomological Collection, Bishop Museum, Honolulu, Hawaii.

This common weevil species was collected mainly on trees and in the forests. Beck found a number of specimens in a cluster of seeds on a leguminous tree, on large leaves of a forest plant, on the bark of a dead tree, and by sweeping the forest shrubs. H. T. Pagden collected *becki* on coconut trees; E. Ramey collected them by sweeping in the forest jungle.

Trigonops platessa Heller

Heller, Verh. Naturf. Ges. Basel XLV, 1934, p. 19

Fig. 32-33-34.

Derm black with cinereous, iridescent and some blue scales. Head slightly wider at base than apex; rostrum as long as wide, sulcus separating head from rostrum, crescent shape; scrobes large, rostral ridge reduced to one-third width of rostrum; scales sparse on rostral declivity; antennae scape large at base, filling scrobel cavity, not reaching middle of prothorax, as large at apex as at base; covered dorsally with blue and green scales and decumbent setae; first funicle joint elongate, greater in diameter than following short round segments, club as long as three preceding segments. Eyes moderately convex, pointed posteriorly. Prothorax considerably wider than long, widest at posterior third, dorsum flat transversely sloping towards apex, margin somewhat irregular due to close rather deep punctures which bear decurved setae; median space slightly keeled, bordered with small black granules, base and apex truncate, slightly constricted near apex. Central portion of disc with small green and blue scales, marginal scales larger and cinereous. Elytra widest at apical fourth sloping to declivity at posterior fourth; pointedly narrowed to apex; intervals 4-5 slightly elevated caudad, more so in males, which results in a longitudinal concavity; stria 10 with small punctures, curved due to lateral emargination of elytra, scales mainly on intervals, striae punctures distinct, with small black granules along side of punctures, female with tuft of setae on suture at declivity. Legs, hind femora not reaching the apex of elytra; club of femora heavily covered by cinereous and green scales, hind tibia straight, middle and front tibiae slightly curved. Dorsal lateral margin of the mesothorax with a prominent conical elevation; ventral lateral portions and posterior margin of ventrites 1-2

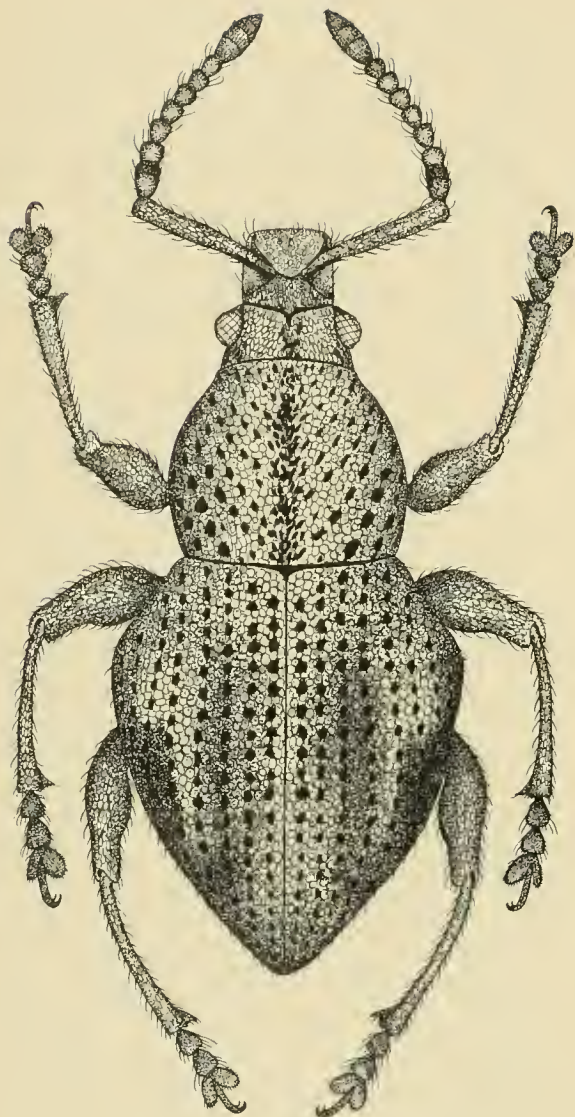


Fig. 32. *Trigonops platessa* Hllr.

with cinereous and green scales, punctures sparse. Ventrites 3-5 sparsely punctuate, with setae on 5.

Length 8.1-9.2 mm; breadth 3.2-4.9 mm.

Type locality: Solomon Islands (Dr. Staudinger and Bang Hass supplied a single damaged specimen.)

Distribution of specimens studied: Guadalcanal: Tengeru River Area, 1944-45 (D E. Beck, Ernest Reimschuessel, E. Ramey, and Doyle Taylor); Tunga River Bridge, and Nalimbu River, July-August, 1960, (Jan Schenk); Honiara District, Kukum, January 27, 1957 (P. G. Fene-more); Wanderers Bay (data and collector not known); Florida Island: April 15, 1944 (Harry P. Chandler).

T. platessa is a common species around the Henderson Field area. Beck, Reimschuessel, Ramey, and Taylor collected 150 specimens. Practically no information dealing with the host plants or the life history of this species is available. Captain Beck did report collecting specimens of *platessa* "on the under-surface of a dead log," "found on all the plants of the forest and on the yellow hibiscus tree," "on the leaves of the torch ginger plant," and, "at random in the forest." Ramey collected many specimens of this species in the "jungle forest."

Since so few specimens of most of the species dealt with are at hand, the study of the genitalia has been limited to a few species. A number of specimens of *platessa* were dissected. The female ovipositor is one of the elongate type. When fully extruded it is as long as the insect abdomen. The ninth segment, valvifer and coxite are partially sclerotised making it possible to have it folded in the body cavity until in use when depositing eggs. The spermatheca of *platessa* is distinctive, differing in detail from that

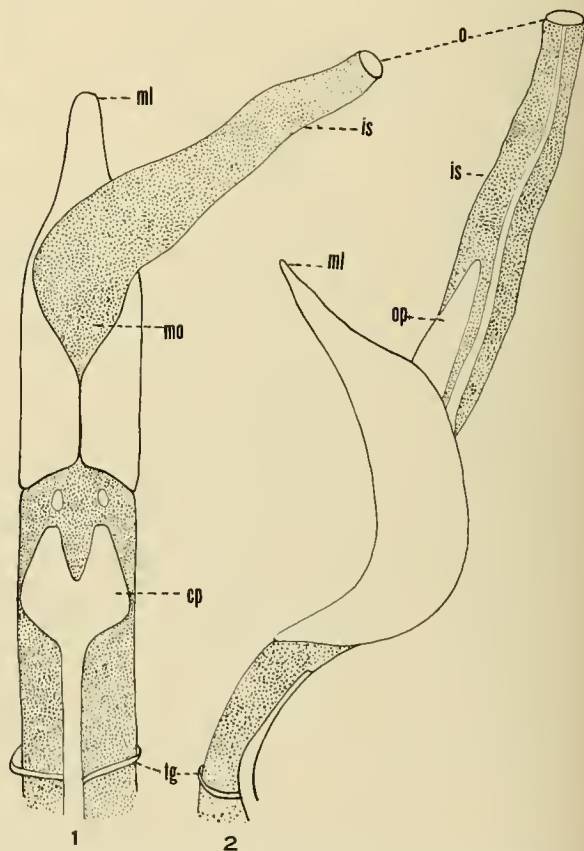


Fig. 33. *Trigonops platessa* Hllr. ♂ genitalia o-orifice of internal sac; ml-median lobe; mo-median orifice; tg-tegmen; op-orificial plate; is-internal sac; cp-cap-pice of tegmen.

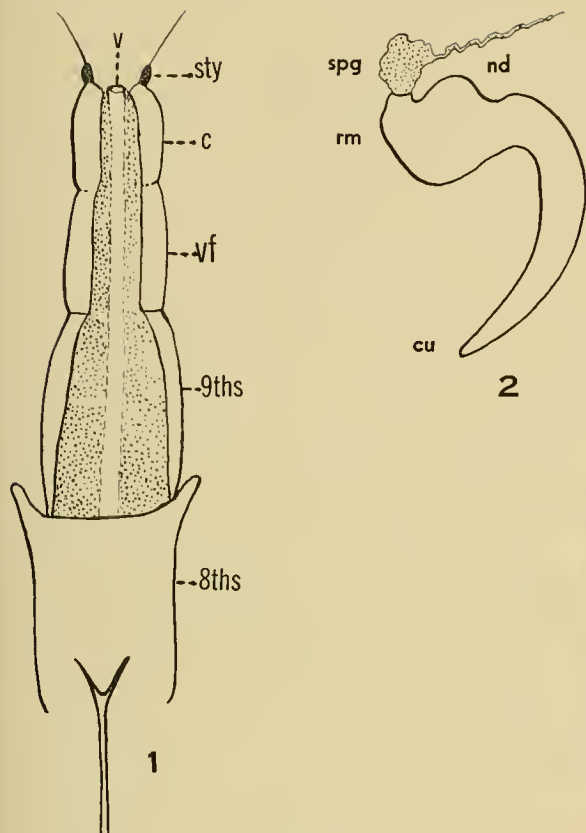


Fig. 34. *Trigonops platessa* Hllr. 1 ♀ genitalia and 2 spermatheca sty-stylus; c-coxite; vf-valvifer; 9ths-ninth sternite; 8ths-eight sternite; spg-spermathecal gland; nd-nodulus; rm-ramus; cu-cornu.

found in other species of this genus. The internal sac of the male genital tube was successfully extruded as shown in Fig. 33.

These structures serve as a pattern of the genitalia found in other species of *Trigonops*.

T. platessa is rather uniform in size, the females a little larger than the males, rostral space between the scrobes narrow; rostral base tumid, sulcus straight, eyes prominent, not conically pointed, prothorax wider than long; elytra widest near the humerus, transversely concave, intervals 4-5 elevated at declivity and with conical elevation on the dorsolateral margin of the mesothorax. This species is similar in many respects to *T. coerulescens*.

Trigonops granulosa n. sp.

Fig. 35

Body derm black, legs, antennae and tip of rostrum reddish-brown, clothed with sparse small round brown and some gray scales.

Rostrum as long as head, separated from head by a lunulate suture; base of rostrum tumid and punctate, corina short terminating at declivity in a small elevation, declivity sparsely punctate and free of scales; rostrum narrow, scrobes small, separated by width of distal end of scape. *Antennae* slender, scape reaching anterior two-fifths of prothorax; funicle segments 1 as long as 2, 3 almost as long as 2; 4-7 mainly obpyriform, club as long as 5-7 combined; small punctures and colorless scales on scape, none on funicle, setae short, bowed and brownish in color. *Head* very rugous, frons concave near junction with rostral suture, forming a shallow depression, small brown scales on elevated thickened lines;

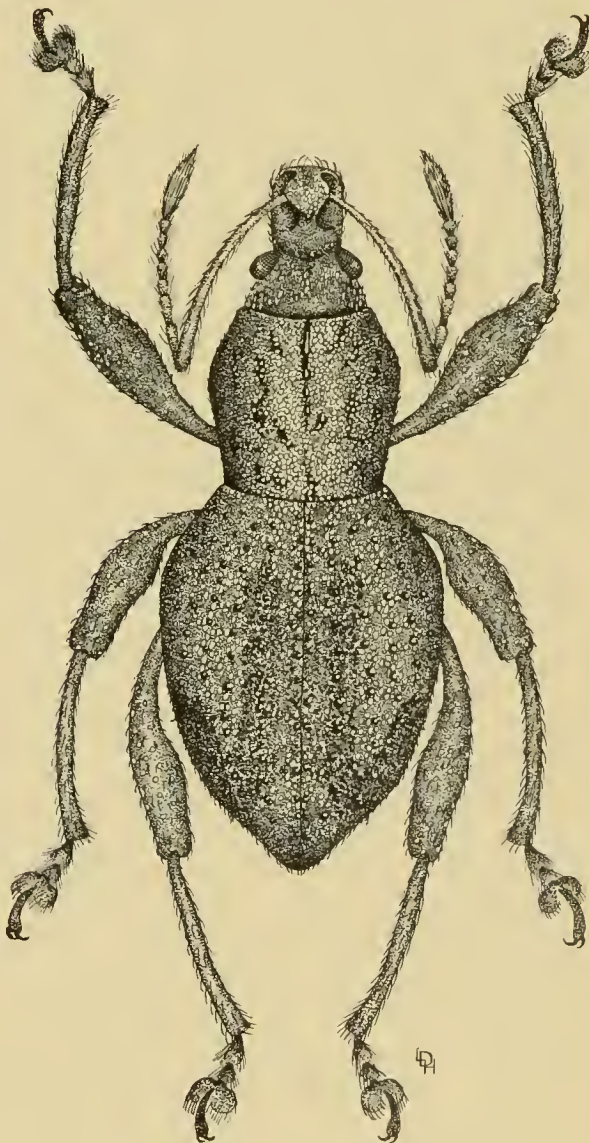


Fig. 35. *Trigonops granulosa* n. sp.

eyes round, slightly conical. *Prothorax* as wide as long, greatest width at middle, base and apex truncate, entire surface granular, each granule with polished apex and separated by deep punctures and lines; brownish, iridescent scales placed irregularly on granules, convex transversely, sloping longitudinally from center of disc to apex and base. *Elytra* subovate, three-fourths as broad as long, broadest before middle, flat or concave on basal disc, becoming concave along elytral suture and between fourth intervals, which in some specimens become slightly to greatly elevated at declivity and rather precipitous in some others; elytra emarginate near acuminate apex; 10 striae, tenth narrow and close to ninth, striae punctate; intervals narrow, each with a row of black, shining granules, scales few, brown to ididescent in color. *Legs*, femora not extending beyond end of elytra; club near apical end of femora; brown scales and short white setae on femora and tibia. Ventrites 1-2 connate except laterally free from scales in middle, ventrites 3-5 narrow, with few or no scales.

Length 4.8-6.0 mm.; breadth 2.5-3.1 mm.

Type locality: Solomon Islands: Holotype, Florida Island, April 4, 1944 (Harry P. Chandler); Allotype: Florida Island, April 4, 1944, 100 feet, 4-paratypes, Florida Islands, April 15, 1944 (Harry P. Chandler); 1-Florida Island, Tulagi, January, 1933 (R. A. Lever); 1-Isle of Savo, April 25, 1922 (E. A. Armytage); 1-Kalambangara Island, April 4, 1922 (E. A. Armytage); 1-Guadalcanal Island, Upper Matanikau R., Jan. 26, 1958 (P. G. Fenimore); 3-Guadalcanal Teneru R., 1944 (D. E. Beck), 1-Guadalecanal Teneru R., 1945 (E. Reimschuessel); 6-Guadalcanal Island, (Suta-Gold Ridge) Jonapau Mt. 1000 M., June 29, 1966 (J. L. Gressitt). 1-Guadalcanal Island Gold Ridge, March 21, 1955 (E. S. Brown); 1-Guadalecanal Island, Popaner, 3000-5000 feet, December 1934 (R. A. Lever, C. Bird).

Holotype, allotype and four paratypes deposited in the Entomological Type Collection, Brigham Young University, Provo, Utah. Paratypes deposited in the Entomological Collections of the British Museum of Natural History, London; Bishop Museum, Honolulu, Hawaii; U. S. National Museum, Washington D.C., and California Academy of Sciences, San Francisco, California. Captain Beck collected two specimens of *granulosa* under an overturned log in a cut over area near the Teneru River on May 30, 1944. No other information is available concerning the habitat or conditions under which specimens were collected.

There is considerable variation in the shape of the elytra of this species. The slender, reddish-brown antennae, shape of the eyes, furrowed frons, rugose prothorax, granules and brown scales on prothorax and elytra serve to separate *granulosa* from other species of *Trigonops* of this study.

Trigonops isabellae n. sp.

Fig. 36

Body derm black and reddish-brown, legs and antennae brown with scales light green and some brownish and cupreous. *Rostrum* short and narrow, slightly longer than head, scrobes large, separated by narrow ridge, which is elevated at junction with declivity. *Antennae* scape narrow at base, expanded a little at apex, with some small scales, and low-lying setae; sulcus V-shaped, laterally joining posterior portion of scrobes. *Head* rugose densely covered with pale green and cupreous scales; a distinct line, separating scales on frons, extends from acture angle of sulcus towards vertex of head; eyes practical-

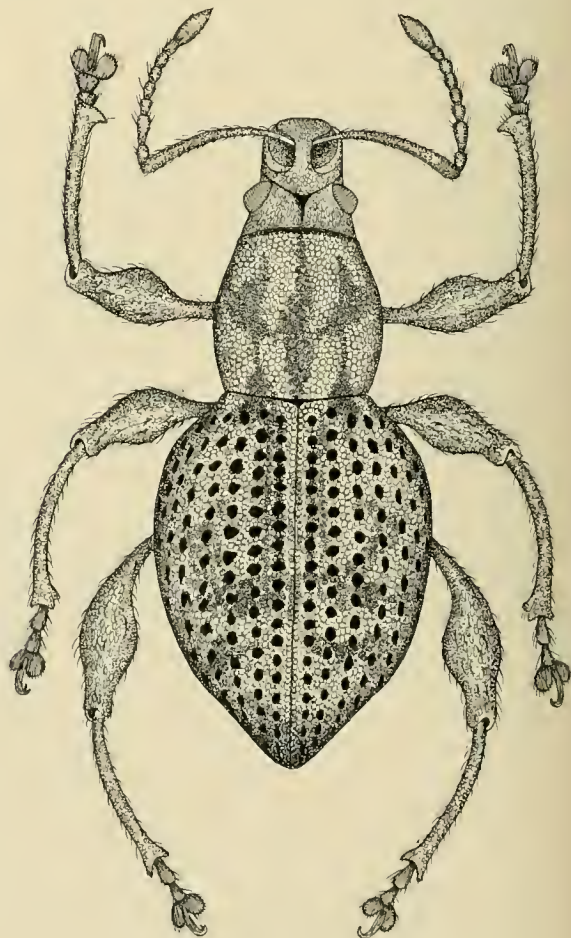


Fig. 36. *Trigonops isabellae* n. sp.

ly round, only slightly conical, separated from the rostral sulcus by a row of scales. *Prothorax* as long as wide, greatest width at middle, gradually rounding from middle to apex and base, slight constriction near apex; base and apex truncate; transversely convex; dorsum punctate, granulated, and covered with cupreous, pale green and brown scales; pattern as shown in Fig. 36. *Elytra* ovate, with 10 striae, striae 10 complete, but narrow and very near edge of elytra; greatest width near base; punctures deep with small granule on septa partially obscured by scales; scales mainly pale green with some brown and iridescent ones near base and on disc of elytra, transversely convex tapering from declivity to a point at apex. *Legs*, femora and tibia densely covered with round, pale green scales and white low-lying setae. Venter with scales, ventrites 1 medium area with few deep punctures, devoid of scales; 2 lateral and posterior portion with small scales and setae, 3-4-5 without scales and setae.

Length 5-6.9 mm; breadth 2.5-3.1 mm.

Holotype ♀ Solomon Islands; Ysabel Island, Margine Lagoon, February 8, 1955 (E. S. Brown); allotype ♂ same data as holotype. Two paratypes same data as holotype; six paratypes Ysabel Island, Huhurangi, February 18, 1956 (E. S. Brown); eight paratypes, Guadalcanal Island, 1944 (D. E. Beck); one paratype Florida Island, March 1945 (John Stuntz); one New Georgia Island, Segi; no other data.

Holotype, allotype and eight paratypes deposited in the Entomological Collection, Museum of Natural History, London, England; two paratypes, Bishop Museum, Honolulu, Hawaii; two paratypes, Entomological Collection, California Academy of Science, San Francisco; two paratypes, Entomological Collection, U.S. National Museum, Washington, D.C.; eight paratypes in the Entomological Collection, Brigham Young University, Provo, Utah. *T. Isabellae* is characterized by a short, slender rostrum, scape of antennae slender, small subconical round eyes separated from the rostral suture by a row of scales, pale green and iridescent scales on the body, scale pattern on the prothorax and elytra, (Fig. 36), with deep rather widely separated punctures on the elytra, and on obovate body.

Trigonops carinithorax Heller

Heller, Verh. Naturf. Ges. Basel XLV, 1934, p. 20

Fig. 37

Derm black with ash-colored scales. Rostrum as long as head, ridge with sharp carina, termi-

nating in a slight elevation at declivity; declivity finely punctured, with small gray scales near apex; sulcus curved, extending to posterior border of scrobes; antennae scape bowed near origin, same diameter throughout, reaches middle of prothorax, funicle segments pyriform, 1-2 longer than discal ones. *Head* sloping rapidly from apex to sulcus, short carina from middle of frons to sulcus, lightly rugose, small granules densely covered with gray scales. *Eyes* round, convex, placed well down on lateral side of head, separated by 1 mm from rostral sulcus. *Prothorax* wider than long, subcircular, slightly convex transversely at middle, sloping longitudinally from center to base and apex, constricted near apex; base and apex truncate, densely covered with small scales and decumbent setae which obscure to some extent granules and punctures, lateral areas deeply punctate and with some iridescent scales; median carina shiny black, not so densely covered with scales as balance of prothorax. *Elytra* with greatest width near

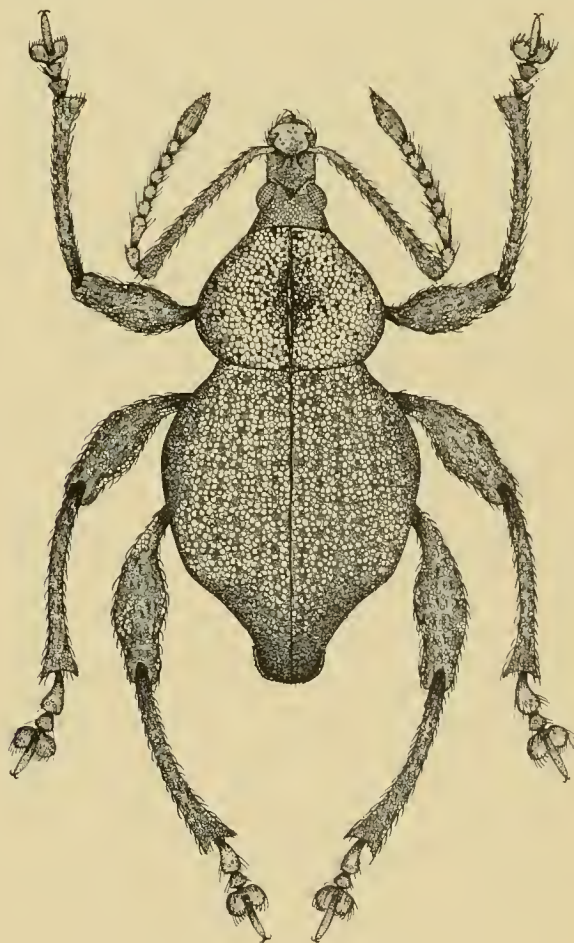


Fig. 37. *Trigonops carinithorax* Hllr.

humerus, interval 6 elevated near declivity, emarginate at posterior area, termination rather acuminate, sutural area slightly concave, striae punctate, intervals densely covered with scales; female with tuft of setae on declivity; transversely convex and only slightly elevated. *Legs*, femora extending to tip of elytra, femora and tibia densely covered with ash-colored scales and setae, ventrites 1-2 covered with scales laterally, free from scales in median area, no punctures and only a few setae; 1 with greater breadth than 2; 5 as wide as 3-4.

Length 8.5-9.8 mm; breadth 3.5-5 mm.

Type locality: Solomon Islands: Bougainville Island.

Specimens studies: One cotype from Bougainville Island loaned from Museum für Tierkunde in Dresden, and five other specimens from Bougainville; 1 Kieta IX-X-1937 (J. L. Froggatt); 1 Simba Mission, VI-28-VII-22, 1956 (B. J. Ford, Jr.); 1 Bougainville Is. VII, 1945 (A. J. Walz), and 3 Bougainville Is. - no other data.

T. carinithorax is readily separated from other species included in this study by the roundish ash-gray scales, shape and width of the prothorax, elevated fifth and sixth intervals of the elytra at the declivity, and its size.

Trigonops bougainvillensis n. sp.

Fig. 38

Dern black, with small, round, green scales on body, antennae, legs and venter, except medial area of ventrites 1-2 and all of 3-5.

Head as long as rostrum, separated from rostrum by a curved sulcus, eyes prominent and round; trace of a carina extending from apex to rostral suture ending in a fovea; scales thickly placed around eyes and rugose lateral and venter areas. *Rostrum* deeply incised by scrobes with trace of precipitous carina, terminating in an angular elevation at junction with the declivity, declivity precipitous, punctured near apex and devoid of scales. *Antennae* scape deeply punctured and with long, light-colored and short, dark setae; scape reaching middle of prothorax; distal expanded; funicle as long as scape, segments 1-2 equal in length, combined as long as 3-5, the latter pyriform, 7 smaller and more elongate, club sericeous, slightly longer than segments 5-7 combined. *Prothorax* 3.5 mm wide, 3 mm long, greatest width at middle; apex and base truncate; transversely slightly convex; constricted near apex, median carina prominent,

elevated some at apical end; medial area with few scales, discal surface with granules and punctures, which are largely obscured by scale covering. *Elytra* widest near base, gradually narrowing to apex, surface flat except for a slight elevation of intervals 5-6 at declivity, striae with punctures, each puncture contains a granule with small setae, intervals with scales and very small granules, interval 9 coalescing with other intervals at apex, forming a raised strip, densely covered with light setae and scales. *Legs*, femora reaching apex of elytra; femora and tibia densely covered on dorsum with scales and short setae; clubs of femora median-sized and strongly rugose on inner surface. Ventrites 1-2 devoid of scales in median area.

Length 8.1-12.9 mm; breadth 3.5-5.1 mm.

Type locality: Solomon Islands: Bougainville Island, Boku, VI-4-1956 (J. L. Gressitt). Type deposited in the Entomological Collection, Bishop Museum, Honolulu, Hawaii. Paratypes in the Bishop Museum; British Museum of Natural History, London, England, and Entomological

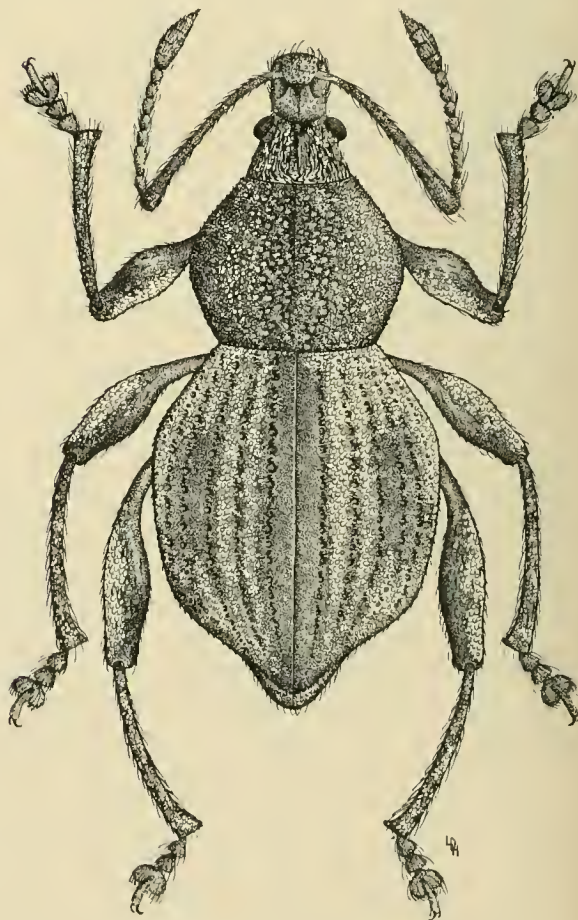


Fig. 38. *Trigonops bougainvillensis* n. sp.

Collection, Brigham Young University, Provo, Utah.

Remarks: *T. bougainvillensis* is closely related to *T. carinithorax*. The scale color and pattern, size, reddish color of the legs in some specimens, the small funicle segments, and the shape of the elytra of *bougainvillensis* may be used to separate these two species.

Trigonops guadalcanalensis n. sp.

Fig. 39

Derm black with small, irregularly shaped white and iridescent scales; prothorax flattish without a medium carina, but with small black granules, irregularly placed; scales evenly distributed over dorsal surface.

Head and rostrum shorter than prothorax, separated from rostrum by a V-shaped sulcus. Rostrum narrower than head, with narrow carina

separating scrobes, declivity sparsely covered with white scales. Antennae scape sparsely covered with scales and decumbent setae, proximal end narrow, slightly widening to distal end, reaching to middle of prothorax; funicular segments very similar in shape, first two longer than other segments, clothed with straight black setae, club as long as segments 5-7 combined, thickly covered with white setae. Eyes not prominent, but rather small and evenly convex, placed on lateral portion of head; frons slightly convex, covered with white scales. Prothorax wider than long, base and apex truncate, widest at middle, constriction near apex, base twice as wide as apex, disc flattish, small black granules showing through scale cover, punctures in irregular striae, short, white setae and punctures obscured by scales. Elytra twice as long as wide, widest just anterior to middle, punctures deep, prominent and separated by width of a scale, rows of small closely set scales along elytral suture, small, black granules separating punctures; intervals covered by two rows of scales, tuft of setae on steep declivity in females. Legs, hind femora reaching just beyond apex of elytra, femora black, tibia and tarsus reddish brown, covered with white scales and setae. Ventral surface sparsely covered with white setae and scattered white scales, ventrites 3-5 shorter in length than 2 and devoid of scales.

Length 4.0-4.3 mm; breadth 2.1-2.4 mm.

Type locality: Solomon Islands: Guadalcanal, Tenaru River Area. Holotype ♀, Guadalcanal Islands, Tenaru River Area, 1944 (D Elden Beck); Allotype ♂, Guadalcanal Island, Tenaru River, 1944 (Ernest Reimschuessel); 32 paratypes same data as holotype and allotype; two paratypes Guadalcanal Nalimbu River, July 4, 1960 (Jan Schenk); six paratypes, Guadalcanal, Lunga River Bridge, August 23, 1960 (Jan Schenk); one paratype, Guadalcanal, Honiara Bot. Gardens, June 16, 1961 (Jan Schenk); one paratype, Savo Island (no other data); one paratype, Russell Island, Lingatu, February 9, 1936 (R. A. Lever); one paratype, Bougainville, Naval Air Base, April 1945 (G. E. Bohart); one paratype, Guadalcanal, Gold Ridge, 1-2000 feet, September 21, 1958 (P. G. Fenemore); one paratype, Guadalcanal Iiu Farm, December 26, 1953 (J. D. Bradley); one paratype, Guadalcanal, Kukum, March 23, 1958 (P. G. Fenemore); and five paratypes, Guadalcanal, Matengo, March 1933 (R. A. Lever).

The holotype, allotype and 18 paratypes are deposited in the Entomological Type Collection of the Brigham Young University; nine para-

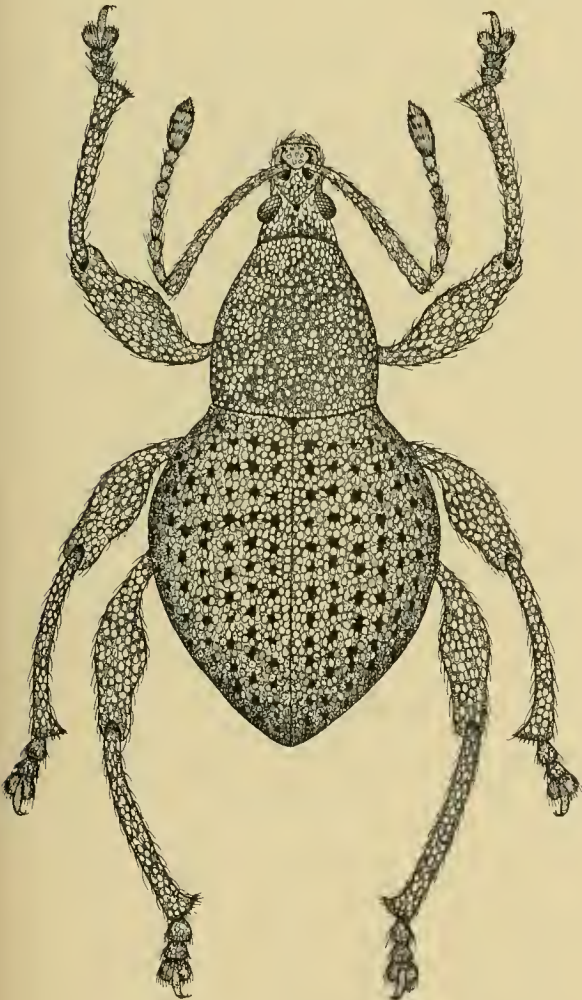


Fig. 39. *Trigonops guadalcanalensis* n. sp.

types deposited in the Entomological Collection, British Museum of Natural History, London, England; six paratypes in the Entomological Collection Bishop Museum, Honolulu, Hawaii; three paratypes in the Entomological Collection U. S. National Museum, Washington, D. C.; three paratypes in the Entomological Collection, California Academy of Sciences, San Francisco.

Captain Beck collected this species under a coral-colored fungus growing on a dead tree in a moist jungle habitat; he also obtained it from sweeping a grassy plot a few yards from the beach and near a jungle thicket.

T. guadalcanalensis is a small species, clothed with a thick covering of pale greenish-white and iridescent scales; disc of the prothorax flattish without a median corina and with small black granules; rostrum and head shorter than the length of the prothorax; antennae scape slender; elytra, greatest breadth near the base, strongly convex transversely and precipitous at the declivity.

Trigonops helleri n. sp.

Fig. 40

Derm of head, prothorax, and elytra black; legs, antennae, and ventrites with some reddish-brown color; scales cinereous.

Head and rostrum as long as prothorax, rostrum as long as head, carina terminating in small elevation; declivity shiny with few shallow punctures and scales. *Antennae* scape reaching middle of prothorax; slightly bowed and expanded at apex; densely covered by scales, light setae; funicle segments 1-3 elongate, as long as 4-7 combined; club short, as long as segments 6-7. *Eyes* round, convex but not as conic as some other species of genus. *Frons* and *vertex* rugose, fovea at apex of rostral suture. *Prothorax* as wide as long, widest just back of middle, apex narrower than base; waved elevated lines lateral and discal surface, punctures and granules interspersed between wrinkles; median carina sparsely covered with scales; base and apex truncate. *Elytra* longer than wide, acuminate; greatest width 2.9 mm transversely convex; obovate, striae punctate, with black shiny granules on spaces between punctures, intervals thickly covered with scales, especially along elytral suture, emarginate near apex. *Legs*, hind femora not reaching apex of elytra; femora and tibia, dorsally densely covered with light setae and scales, hind tibia straight, fore and middle tibia bowed; ventrites 1-2 reddish brown, laterally covered with light setae and scales, center portions shiny,

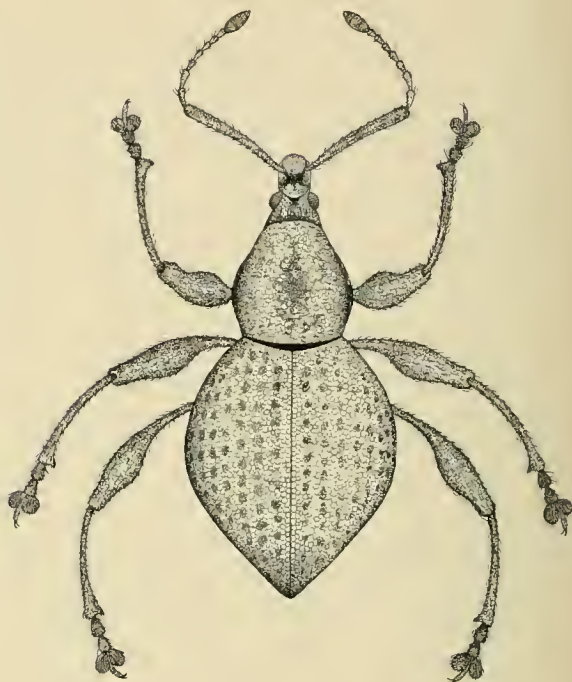


Fig. 40. *Trigonops helleri* n. sp.

with few small setae, ventrite 5 longer than 3-4 combined, densely covered along apical margin with light setae.

Length 3.5-5.5 mm; breadth 2.0-3.5 mm.

Type locality: Solomon Islands: Kolombangara Island 7-II-1922 (E. A. Armytage). *Specimens studied*: Holotype and two paratypes, Kolombangara Island, VI-1922 (E. A. Armytage); three paratypes, Kolarbangara Island, Iri-iri, 27, III, 1958 (P. G. Fenemore); 12 paratypes New Georgia Group, N. Georgia Island, Munda, I-30 m. July 20, 1959 (J. L. Gressitt); three paratypes, New Georgia Group, Kolombangara Island, Kukundu, S. W. Coast, 1-12 m., July 8-II, 1959 (J. L. Gressitt).

The holotype and four paratypes have been deposited in the Entomological Collection, British Museum, Natural History, London. Six paratypes placed in the Entomological Collection, Bishop Museum, Honolulu, Hawaii. Three paratypes in the Entomological Collection, U. S. National Museum, Washington, D. C. Two paratypes in the Entomological Museum, California Academy of Science, San Francisco, California, and six paratypes in the Entomological Type Collection, Brigham Young University, Provo, Utah.

Throughout this study an attempt has been made to get host plant information for each of the species dealt with. The most complete available report on the host plants of a species of

Trigonops was made by J. L. Gressitt who collected many specimens of *helleri* on N. Georgia Islands. Dr. Gressitt found *helleri* on *Flagellaria*, a Flagellariaceae, one of three known species of a climbing monocot, which is distributed from Africa to Formosa, Indomalasia, Australian, and the Solomon Islands. He also collected it on *Freyinetia*, a Pandanaceae, a monocot and one of the screw pines; on *Acalypha*, a Euphorbia; *Glochidion*, another Euphorbiaceae; *Heliconia* and palms.

I take pleasure in dedicating this species to the memory of K. M. Heller of Dresden, who contributed so much to the knowledge of the South Pacific weevil fauna.

Trigonops seriatopunctata Heller

Heller, Arb. Morph. Taxon. Ent. II, 1935, p. 269

Fig. 41

Derm black with chalky white scales and unpunctured prothorax. Head and rostrum clothed with light-colored distinctly separated scales; rostrum with narrow carina about breadth

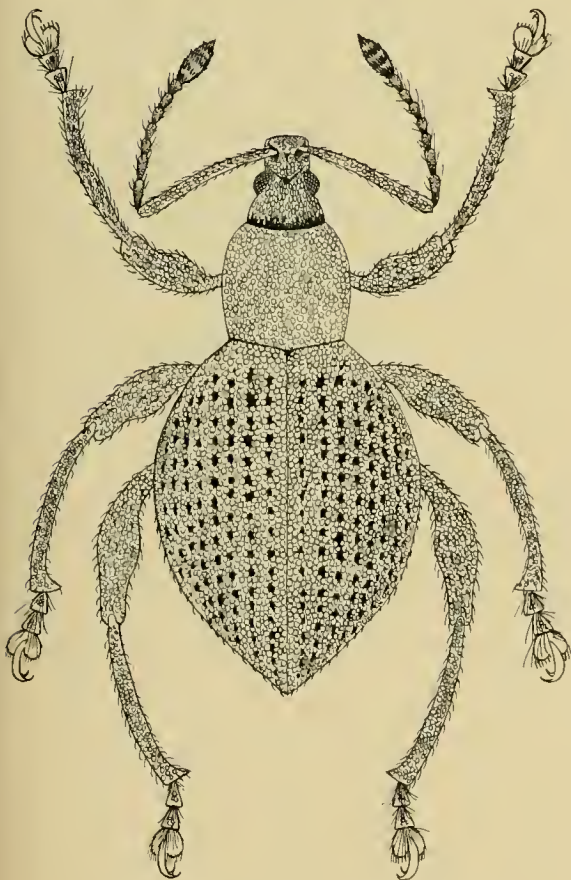


Fig. 41. *Trigonops seriatopunctata* Hllr.

of scape of antennae and without an elevation at junction with declivity; antennae scape reaching middle of prothorax; segments of funicle 1-2 elongate, 3-5 obovate and about equal in length; club length that of segments 4-7. Eyes hemispherical in shape; rostral suture V-shaped and distinct. Prothorax width 1.3 mm; length 1 mm; no median carina, disc flat, evenly covered with roundish pearl-colored scales, crescent apical area with fine setae; base slightly angular; disc and lateral surface without punctures; or median modification, scales uniformly but separately placed. Elytra widest at middle, evenly sloping to a point at apex; surface of elytra flat, intervals between punctures not elevated; base of elytra not punctate, intervals approximately twice diameter of punctations which bare small setae. Legs, femora of metathoracic legs stout, but clubs only moderately enlarged, not reaching apex of elytra, ventrites 1-2 bowed; 3-5 straight; punctation and scales sparse.

Length 4.0-5.0 mm; breadth 2.0-2.3 mm.

Type locality: Solomon Islands: New Georgia, Pauru 1931 (Fr. Malches). The specimens from which this description and drawing was made came from Solomo I. Georgia: Pauru, Fr. Malches, Coll. 1931. These are the only specimens of this species available. Dr. Wilhelm Gotz provided by loan specimens of *seriatopunctata* for my study. They are labeled as cotype specimens of *Trigonops seriatopunctata* Heller.

Trigonops dilaticollis Gunther

Gunther, Mitt. Deut. Ent. Ges. Vol. 8, -3, 1937.

Fig. 42

Derm black covered with small round gray-brown scales, prothorax strongly emarginate at the base and flattened. Rostrum as long as head, carina fine, terminating at declivity in a small angular elevation, declivity precipitous, devoid of scales except near elevation of carina, scrobes large and open, separated by narrow carinal ridge; antennae scape expanding in diameter from origin to apex, reaching to middle of prothorax; funicle segments 1-2 elongate, 3-6 globose, 7 more elongate, club as long as segments 5-7. Eyes large, round, well down on lateral portion of head, and rather flattish, rostral base along curved sulcus rather tumid. Prothorax, wider than long, widest at the outer angle of basal emargination, apex and base truncate and equal in width; surface with white scales, flat, with small punctures and granules with white setae issuing from side of each. Elytra with greatest breadth before middle; striae punctate,

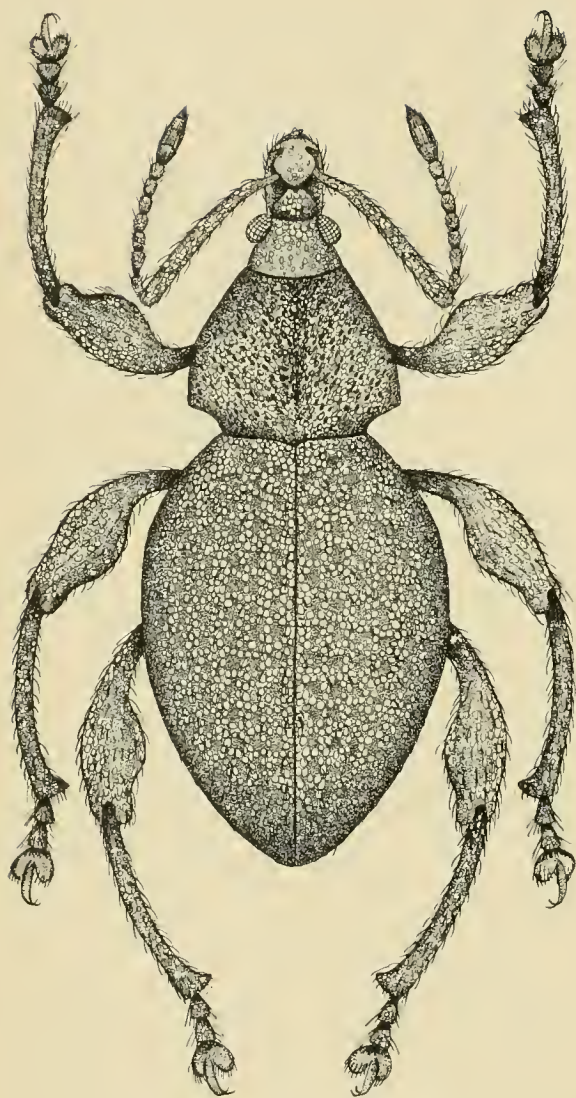


Fig. 42. *Trigonops dilaticollis* Gunther

interval and interpunctate surface covered with white and brown scales; surface of male slightly concave longitudinally, female surface slightly convex transversely and with a tuft of setae at declivity; decumbent white setae present from declivity to pointed apex. *Legs*, femora not reaching apex of elytra; dorsal surface of femoral club densely covered with white scales. Ventrites 1-2 connate, punctate and with scales on lateral portions, median area glabrous. Ventrites 3-4 without scales and setae, ventrite 5 with white setae.

Length 5.3-6.8 mm; breadth 3.1-3.8 mm.

Type locality: San Cristobol Is., Kira Kira, May 2, 1935.

Specimens studied: San Cristobol Is., Kira Kira, May 5, 1934 (R. A. Lever), S. Malaita,

Mukka, May 5, 1934 (R. A. Lever), Ugi Is., May 6, 1934 (R. A. Lever).

T. dilaticollis is a distinctive species because of the basal emargination of the prothorax, flatness of the prothorax and elytra; position and shape of the eyes, large open scrobes, narrowly separated by the rostral carina; prothorax covered with closely placed granules and punctures; ventrites 1-2 being connate. Gunther suggested that *Trigonops platessa* and *T. carinithorax* are related to *dilaticollis*. There are some resemblances, but many differences.

Trigonops vitticollis Fairm.

Fairmaire, Ann. Soc. Ent. Belg. XXVII, 2, 1883, p. 34

Derm, dark brown, approaching black, with ash-colored scales; body oval, oblong and rather convex. *Head*, vertex darker, median portion of rostrum with carina; scrobes large, antennae scape long, first funicle segment elongate, second segment shorter, others unequal, acute. *Eyes* convex, but not pointed. *Prothorax* narrow longitudinally, greatly narrowed towards apex; median line of a smoky or blackish tinge with here and there on lateral margin of elytra brownish spots or centers of scales and setae; punctures with scales in rosette-shape, median granules bare and irregularly placed. *Elytra* ovate, short, apex obtusely acuminate; base not at all latioribus, middle enlarged, intervals not punctured, striae deeply punctured continuously to apex; level between interstices; prosternum narrows, but coxa cavities by no means contiguous; mesosternum short, lato; metasternum punctate; abdominal base obtusely truncate, thinly covered with rigid bristles on middle, lateral margins grossly punctate, suture between ventrites 1-2 obliterated, ventrites 3-4 narrow, femora club robust.

Length 7 mm.

Type locality: Duke of York Islands.

Fairmaire comments that except for the shape of the eyes this insect species belongs to the genus *Trigonops*. The longitudinal brown markings of the prothorax readily distinguishes it. This species is unknown to me.

Trigonops notaticollis Heller

Heller, Wien. Ent. Zeit. XXIX, 1910, p. 190

Fig. 43

Derm black or reddish-brown, covered by blue-gray scales, apical rostral carina elevated, elytra flattened, lateral costa 7 and 9 elevated.

Fig. 43. *Trigonops notaticollis* Hllr.

Rostrum about as long as wide, thickly covered with scales, separated from head by a curved suture. *Antennae* reddish-brown, all segments with setae, 1-2 oblong, 3-7 submoniliform, club oblong-oval; scape wider at apex than at base. *Head* short, broad, covered with scales, short setae issuing from punctures. *Eyes* curved, almost spherical, their apex shifted toward rear. *Prothorax* broader than long, base, and apex truncate, constricted near apex, deep punctures surrounded by scales in a rosette shape; two basal black markings. *Elytra* short, egg-shaped, above flat lateral edges with elevated costa, widest before middle, punctures bearing short setae, scales compact on costal intervals. *Legs* reddish-brown, femora not reaching apex of elytra; heavily covered with scales, and short, light colored setae, under side sparsely covered with scales, punctures few, with white setae; ventrite 2 with greater breadth than 3-4-5; 5 wider than 3-4; a few small white scales and setae on ventrites 3-4.

Length 4.5-5.3 mm; breadth 2.5-3 mm.

Type locality: Tasman Island (R. V. Rennigsen).

Locality: Distribution of the specimens of this study: Solomon Islands; Sikaiana (Stewart Islands), March 23, 1936 (R. A. Lever).

Remarks: The nine specimens used in this

study were compared with the two cotype specimens of *notaticollis* from the Dresden Museum. They agreed perfectly with the Heller specimens. Heller related *notaticollis* to *Trigonops dispar* Jek. Marshall 1956, transferred *dispar* to a new genus *Platysinus* along with five other species that had been in the heterogeneous *Trigonops* prior to Marshall's study.

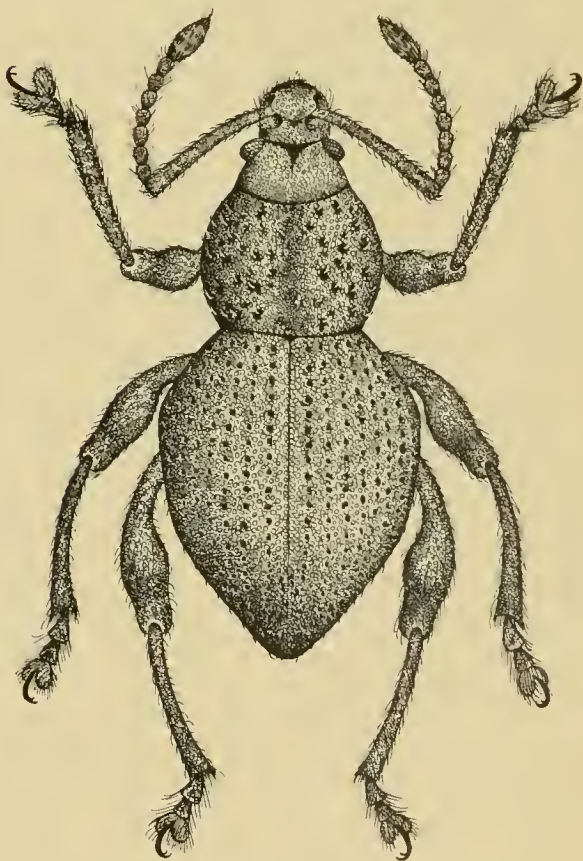
Trigonops forticornis Heller

Heller, Wien. Ent. Zeit. XXIX, 1910, p. 187, Fig. 3.

Fig. 44

Derm black with some dark brown to reddish color on legs and elytra, scales pale green with some bluish ones on legs.

Rostrum as long as it is wide, scrobes deep and wide, head separated from rostrum by a rather straight sulcus; antennae scape of equal diameter throughout, but bent slightly at its proximal end; segments 1 and 2 of funicle equal in length, conical and approximately one and one-half times as long as wide, other segments somewhat spherical, not as long as wide, cov-

Fig. 44. *Trigonops forticornis* Hllr.

ered with black setae and some blue-green scales; club with gray setae. *Head* widening from rostral suture to base, scales sparse on lateral and medial areas; eyes contiguous with rostral suture, not so prominent and less pointed. *Prothorax* wider than long, constricted towards apex, widest at middle, base and apex truncate and equal in width; disc rather flat, median area with few scales, but with small black tubercles, punctures deep, centered with decumbent white setae. *Elytra* widest just back of base, tapering to apex, stria 10 complete with small punctures, punctures on disc large, surrounded with a rosette of pale scales, female with slight concavity of disc near declivity and a tuft of setae on posterior declivity of elytra. *Legs* reddish-brown in color, posterior femora not reaching tip of elytra; underside sparsely clad with green scales; metasternum, ventrites 1-2 with few scales in center portion, these areas rather glabrous with few small punctures and short white setae.

Length 7.0-7.2 mm; breadth 3.4-3.7 mm.

Type locality: Solomon Islands (Russell Island ?) VII-VIII, 1909, W. W. Froggatt (Sideny).

Distribution of specimens studied: Guadalcanal, 2 ♀♀ Tenaru River 1945, G. E. Bohart; 1 ♀ Tenaru River, 1944, Doyle Taylor; 3 ♀♀ Malaita, Auki, IX-21-1957; 2 ♂ Malaita; Tangtatau, IX-25, 1957; 2 ♂ Malaita; Andalimu Nagara-fata, S. W. Fiu River.

Trigonops gressitti n. sp.

Fig. 45

Derm black with green scales in stripes on prothorax and transverse patches on elytra. *Rostrum* short and narrow, slightly longer than head, scrobes large, ridge with an acute carina terminating in an elevation at declivity; declivity punctured and with a few scales on apex, scape narrow, bowed, expanded a little at apex, covered with green scales and black setae, reaching a little beyond middle of prothorax; funicle slightly longer than scape, segments elongate, 1-2 longer than segments 5-6-7 combined, densely clothed with white setae. *Head* wider than long, rugose with few small punctures at apex, covered with scales; a deep sulcus separates rostrum and head; eyes prominent, convex roundly subconical, highest point behind middle; placed low on genae, dorsal space between eyes considerably greater than diameter of an eye. *Prothorax* longer than wide, convex at apex which projection covers over venter of head to some extent, restricted slightly near apex, base

truncate, widest back of middle; dorsum flat longitudinally, with a strip of green scales on either side of median line, disc and upper pleural area with deep pentagonal shaped punctures. *Elytra* plump ovate, widest before middle, convex transversely, dorsum flat yet sloping from middle to front and back, striae with punctures confined within septa and interval walls, latter covered with small, round granules and some green scales; ♀ with tuft of setae on declivity, apex of ♂ produced downward more than in ♀. Stria 10 very close to 9 posteriorly; a shiny glabrous area on intervals 3-4 where metathoracic femora impinges on elytra. *Legs* black, femora extending beyond apex of elytra; dorsum of femora and tibia covered with green scales; venter and lateral portions of ventrites 1-2 and 5 covered with green scales and setae, deeply punctured; ventrites 3-4 narrow and free from scales and setae.

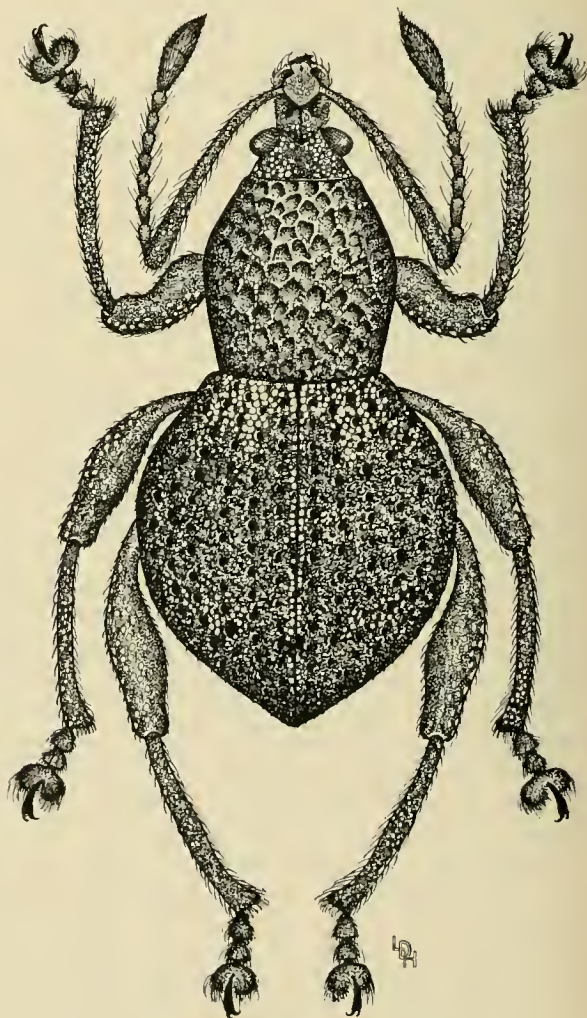


Fig. 45. *Trigonops gressitti* n. sp.

Length 4.8-6.1 mm; breadth 2.6-3.6 mm.

Type locality: Solomon Islands; Holotype ♂ Bougainville (S.) Kokure, Nr. Crown Prince Rd. 900 m. April 8, 1956 (J. L. Gressitt); Allotype ♀ same locality and date; 10 paratypes same locality and data; two paratypes Bougainville (S.) Boku, 50 m. April 5, 1956 (J. L. Gressitt); one paratype Bougainville, April 20, 1944 (A. B. Gurney).

Holotype, allotype and 2 paratypes deposited in the Entomological Collection Bishop Museum, Honolulu, Hawaii; two paratypes in the Entomological Collection, British Museum of Natural History, London, England; two paratypes in Entomological Collection, U. S. National Museum, Washington, D. C.; one paratype in Entomological Collection California Academy of Science, San Francisco, California; and four paratypes in the Entomological Type Collection, Brigham Young University, Provo, Utah. Some of the specimens are rubbed.

T. gressitti is characterized by the large angular punctation of the prothorax; the large eyes, base of the rostrum tumid, and long antennae clothed with scales and black setae.

I am pleased to name this species in honor of J. Linsley Gressitt of Bishop Museum who has done so much to add to the knowledge of and collecting of the insect fauna of Oceania.

Trigonops gloriosa n. sp.

Fig. 46

Derm black, with a uniform pattern of small green scales on rostrum, antennae, head, prothorax, elytra, and legs; devoid of scales on vertex of head, a broad medial area of prothorax and a band across middle and declivity of elytra.

Rostrum, base one-half as wide as base of head, parallel sides and longer than head; suture separating head from rostrum, U-shaped and distinct; apex of rostrum scaleless, scrobes well-developed. *Antennae* with scape slender, enlarged at apex, reaching beyond middle of prothorax, funicle as long as scape, segments 1 and 2 as long as segments 3-6 combined, segment 1 broader, but shorter than segment 2; club as long as segments 4-7. *Head*, eyes placed low on head, in contact with rostral suture, large for size of insect, oval in shape; base of head twice width of apex. *Prothorax*, base and apex truncate, wider than long, greatest width before middle; disc convex, punctures deep, large, angular in shape, and devoid of scales. *Elytra*, one and one-half times as long as wide, greatest width at middle, base truncate, elytral stria 10 approach-

ing closely to 9 posteriorly; punctures deep, a band of small green scales extend along base to lateral margin of elytra, uniting with a band of scales which extend backward to apex; along elytral suture and across declivity bands of scales, otherwise black punctured surface of elytra is glabrous. *Legs*, hind femora reaches beyond tip of elytra; dorsal surface of femora and tibia

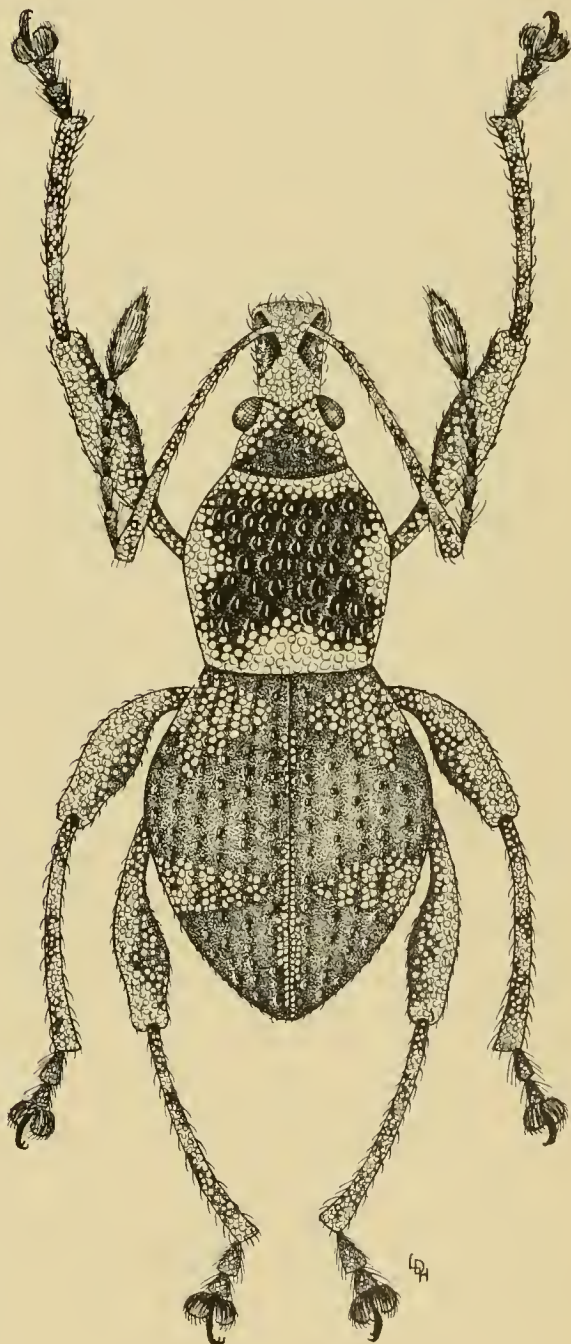


Fig. 46. *Trigonops gloriosa* n. sp.

covered with scales. Under side of specimen clad with green scales except ventrites 3-5.

Length 3.1 mm; breadth 1.5 mm.

Type locality: Solomon Islands; Bougainville, Kokure, 600 m. June 14-17, 1956 (E. J. Ford, Jr.); Specimens studied: Holotype and three paratypes. Holotype deposited in the Entomological Collection of the Bernice P. Bishop Museum, Honolulu, Hawaii, one paratype in the Entomological Collection, British Museum of Natural History, London, England; 1 paratype in the

Entomological Collection, U. S. National Museum, Washington, D. C.; and 1 paratype in the Entomological Collection, Brigham Young University, Provo, Utah.

Remarks: This species is similar in size to *T. minuta*, but differs in scale pattern, lacks the circular decumbent setae on the scape of the antennae and the spine on the humeral angle. The prothorax is convex with distinct deep punctures. The rostral carina is longer and without an apical elevation.

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**Brigham Young University
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**NESTING ECOLOGY OF
RAPTORIAL BIRDS
IN
CENTRAL UTAH**

by

Joseph R. Murphy, Franz J. Camenzind,
Dwight G. Smith, and J. Bradford Weston



**BIOLOGICAL SERIES — VOLUME X, NUMBER 4
OCTOBER, 1969**

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Frontispiece. Thirty-four-day-old Ferruginous Hawks, Thorpe Hills, Utah County, Utah, June 21, 1968. The brood consists of 3 dark-phase individuals and one light ("normal") phase (see p. 34). Photo by J. B. Weston.

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AN INTRODUCTION TO NESTING ECOLOGY OF RAPTORIAL BIRDS IN CENTRAL UTAH

by

Joseph R. Murphy¹

In contrast to many areas of North America, the sparsely-settled Great Basin deserts of Utah still support large and diverse raptor populations. For the past several years these predatory birds have been the subject of intensive studies by personnel of the Department of Zoology, Brigham Young University. The present report deals with the nesting ecology of three of the largest and most conspicuous species. Other studies in progress, to be the subjects of future publications, deal with behavior and ecology of wintering Bald Eagles, causes and influence of raptor mortality, economic relations of Golden Eagles, and factors which control total raptor densities and population dynamics.

DESCRIPTION OF THE STUDY AREA

The research has been conducted within a maximum area of roughly 3000 square miles, involving portions of six counties in central and western Utah. The majority of the field work, however, has been restricted to a smaller area of about 600 square miles at the eastern edge of the Great Basin, lying approximately between North latitudes 40°00' and 40°20', and West longitudes 111°55' and 112°25'. The area includes, from east to west, the following physiographic features (see map, Fig. 2): Lake Mountains, Cedar Valley, southern end of the Oquirrh Mountains and northern portions of the East Tintic Range with intervening groups of hills (Thorpe Hills and Topliff Hills), and a large part of Rush Valley. Elevations range from some 4500 feet above sea level at the west margin of Utah Lake (east edge of study area) to nearly 8000 feet in the Oquirrh and Tintic Mountains. Local relief varies from 3200 feet at Lake Mountain to 1600 feet (maximum) in the Thorpe and Topliff hills.

Geology

The geology of major portions of the study area has been treated by Bullock (1951) for the Lake Mountain vicinity and by Bissell *et al* (1959) for the southern Oquirrh Mountains, Thorpe Hills, and adjacent areas. The structural

geology of the area is characterized by synclinal folds and a series of anticlines developed in a thick series of Paleozoic rocks ranging in age from Lower Cambrian to Upper Pennsylvanian. These strata are folded, faulted, and subsequently eroded in such fashion as to expose numerous cliff lines of resistant limestones alternating with softer shales and sandstones (see Fig. 1). Small exposures of Tertiary volcanic materials, mainly basalts and ignimbrites, are scattered through the area. Quaternary alluvial materials, lacustrine and fluvial in origin, form aprons around the bases of the hills and in the stream valleys and passes. Pleistocene sediments and fan gravels of ancient Lake Bonneville comprise the bulk of these deposits. Most of the present stream drainage in the study area is intermittent or ephemeral; as a result, only thin mantles of recent alluvium are visible.

As is typical of most valleys in the Great Basin, there is very little outside drainage of surface water. For the most part, the surface water is either absorbed by the soil or flows over the surface to the lowest part of the valley, where it is slowly absorbed or evaporated.

Climate

Climatic features of the study area are characteristic of the northern or cold desert regions (Fautin, 1946; Shelford, 1963). Mean annual precipitation is generally less than 15 inches (38 cm) for most of the region, with larger amounts at higher elevations. Distribution of precipitation is very uneven in both space and time. Moisture graphs for the area indicate that most of the precipitation comes during two periods: early spring (March through May) and midsummer (July and August). Significant variations in annual and monthly precipitation patterns are characteristic.

The annual range in temperature may be as great as 65°C in some parts of western Utah, with maxima of 45°C and minima down to -30°C. July is generally the hottest month, with a mean temperature of about 23°C in an "average" year. Wide daily fluctuations in tempera-

¹Department of Zoology and Entomology, Brigham Young University.



Fig. 1. View of a portion of the study area in the Thorpe Hills, Utah Co., Utah, showing resistant limestone strata forming numerous cliff lines appropriate for raptor nesting sites.

ture are also to be expected, amounting to as much as 30° or more in the summer months.

As is true of most arid regions, wind is an important climatic feature in the Great Basin deserts, and combined with the prevailing low relative humidity and dry atmosphere, accounts for the observed high rates of evaporation (Fautin, 1946). The dominant southwesterly winds are particularly strong during the spring months; superimposed upon these and occurring at all seasons, are shallow diurnal mountain and valley winds.

Biotic Communities

A variety of soil types occurs within the area of study ranging from well-drained, gravelly soils on higher ground to fine-textured soils of moderate to high salinity in the lower valleys. This diversity in edaphic conditions is reflected in the plant and animal communities present. In terms of plant dominants, the high ridges and hills support a dwarf conifer community consisting primarily of *Juniperus osteosperma* with smaller amounts of pinyon pine (*Pinus monophylla*) and associated shrubs (e.g., *Cercocarpus*, *Cowania*, *Purshia*). Big sagebrush (*Artemisia tridentata*) is dominant on the well-drained soils of the uplands and lower slopes, while shadscale (*Atriplex confertifolia*) and greasewood (*Sarcobatus vermiculatus*) communities cover large areas of the valley floors. Other prominent shrubs, becoming dominant under certain edaphic and biotic conditions, include rabbitbrush (*Chrysothamnus nauseosus*), four-wing

saltbush (*Atriplex canescens*), winterfat (*Eurotia lanata*), horsebrush (*Tetradymia glabrata*), and bud sage (*Artemisia spinescens*). Originally there were significant quantities of perennial grasses, especially *Oryzopsis hymenoides*, intermixed with the shrubs, but overgrazing and other forms of abuse have drastically altered this situation (see next section).

The principal herbivorous vertebrates include the mule deer, jack rabbit, ground squirrels, kangaroo rats, wood rats, deer mice, pocket mice, grasshopper mice, a number of herbivorous birds (mainly passeriforms), and lizards. Vertebrate carnivores, other than raptors, include coyote, badger, kit fox, bobcat, gopher snake, whipsnake, and Great Basin Rattlesnake. The raptors are particularly well-represented; principal nesting species are the Golden Eagle, Ferruginous Hawk, Red-tailed Hawk, and Great Horned Owl. Represented by smaller nesting populations are the Swainson's Hawk, Harrier, Cooper's and Sharp-shinned Hawks, Prairie Falcon, Kestrel, Burrowing Owl, Screech Owl, and Long-eared Owl. Of these, the conspicuous permanent residents are the Golden Eagle, Harrier, Prairie Falcon, and Great Horned Owl. Important winter residents are the Bald Eagle and Rough-legged Hawk. Little information is available regarding population cycles in prey species and how these may in turn affect the raptor populations.

Human Utilization

Intensive human use of the area extends back a little over a century, and involves three major

activities: livestock grazing, farming, and mineral extraction. Although the main line of the Union Pacific Railroad between Salt Lake City and Los Angeles extends the length of Rush Valley, the four or five towns existing within the study area are all small, with populations of less than 1000.

Important events in western history have influenced the area. Camp Floyd, which supported the largest troop concentrations of any United States military post in the 1850's, was located at Fairfield in Cedar Valley. The route of the Pony Express ran through Cedar and Rush Valleys with relay stations in each valley. Later the booming mining towns of Ophir and Mercur were established in the nearby Oquirrh Mountains. Mining activity has drastically waned in recent years, and the only significant mineral extraction at present involves quarrying of limestone, clay, and calcite; this activity is widespread but pursued only intermittently throughout the study area.

The principal use of the area at the present time is for livestock grazing, notably as winter sheep range. According to Bureau of Land Management personnel, upwards of 40,000 sheep winter in the general study area each year. Such intensive use has had detrimental effects upon forage conditions, and much of the range has been overgrazed. Most of the desirable forage species such as winterfat, bud sage, four-wing saltbush, big sage, and Indian rice grass are reduced both in number and vigor. Less desirable invading species such as halogeton, Russian thistle, matchweed, and cheat grass are now common. Range revitalization programs are presently in effect in parts of the area, utilizing desirable native and introduced species of grasses.

Agricultural practice is limited to the valleys, especially Cedar Valley. Dry-farm wheat raising is the principal activity; the recent introduction of portable overhead sprinkling systems will no doubt extend the acreage involved in wheat production.

A sizable portion of Rush Valley (about 30 square miles) serves as a military reservation for ordnance storage, the Deseret Depot Activity of the Tooele Army Depot.

An additional human activity of increasing importance in recent years is the utilization of the area for sport shooting of rabbits in the winter. Cedar and Rush Valleys usually support dense jack rabbit populations, and owing to their proximity to the urban centers of northern Utah, receive surprisingly heavy hunter visitation, especially on weekends. This activity is

evidently not without consequence for the raptors which present a large and tempting target for the undisciplined gunner. In fact, our observations indicate that shooting is probably a primary cause of post-fledgling raptor mortality in the study area (see Ellis *et al.*, 1969).

ADVANTAGES OF THE STUDY AREA

The area offers a number of substantial advantages to the raptor populations as well as to students of raptor ecology. These may be summarized as follows:

1. Human population density is minimal, and the effects of human manipulation or utilization of the habitat have had no obvious adverse effects on the raptors except for the shooting noted previously.

2. Prey populations appear to be sufficiently large and diverse to support the concentration of different raptors present at optimum densities in all seasons. Although we as yet have no reliable data on cycles or other population dynamics in the prey species, indications are that the raptors readily resort to alternate prey when a prime prey species is temporarily at low levels. The diversity in size and behavior of potential prey species permits allocation of the various raptors to specific trophic niches; this will be elaborated upon more fully in the individual studies.

3. While the nearly treeless, shrub-covered valleys provide adequate hunting territories, the adjacent hills and mountains provide nesting and roosting sites in close proximity to the areas of greatest prey density. Geologically, the sequence of strata in the hills is conducive to providing excellent nesting situations for ledge and hole nesting species. Resistant layers of limestone, alternating with softer beds and generally inclined at an angle, provide the most favorable sites. Tree-nesting species such as the Ferruginous Hawk, Great Horned Owl, and the accipiters frequently utilize the junipers which form an open stand in a characteristic belt throughout the lower elevations of the mountains.

4. Since raptors in the area are in contact with livestock for much of the year, an excellent opportunity is provided for assessment of alleged or actual predation on sheep and other domestic stock. The Golden Eagle, which is the species most often indicted by stockmen, is present year-round in the area; we have been, therefore, paying particular attention to the food habits and economic relations of this species.

THE INDIVIDUAL STUDIES

The individual reports are primarily based upon research conducted by each of the junior authors in the process of obtaining a graduate degree in zoology, under the supervision of the senior author. The papers by Camenzind and Smith deal with species whose biology, although extensively studied in other habitats, is poorly known for desert regions. Weston's study of the Ferruginous Hawk is evidently the first detailed treatment of the nesting ecology of this species; it adds a great deal of new information to existing published accounts of this interesting raptor in such general works as Bent (1937), and Brown and Amadon (1968).

One of the more significant conclusions that may be drawn from a comparison of the three papers relates to trophic niche allocation. Although there is considerable overlap in the kinds of prey items taken, it should be noted that the three species tend to hunt during different parts of the diel cycle. Thus the Golden Eagle is primarily diurnal in hunting activity, the Great Horned Owl is nocturnal, and the Ferruginous Hawk is to a large extent crepuscular, as indicated by the fact that Kangaroo Rats accounted for nearly 45 percent of the prey taken by this species. This utilization of separate hunting periods may be an important factor in permitting populations of several large raptors to coexist

within the same area, utilize a common pool of prey species, and yet avoid direct confrontation or competition.

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NESTING ECOLOGY AND BEHAVIOR OF THE GOLDEN EAGLE. *AQUILA CHRYSAETOS L.*

by

Franz J. Camenzind

INTRODUCTION

The Golden Eagle, *Aquila chrysaetos canadensis* Linn., is facing extinction in much of its range. In the Western Hemisphere its distribution is restricted primarily to the mountainous regions west of the 99th meridian, from extreme northern Alaska to northern Mexico (Hobbie and Cade, 1962) and from timberline in Colorado to below sea level in Death Valley, California (Summer, 1929a).

Although a Federal Law was enacted in 1962 protecting this species, it continues to suffer losses through illegal killing and the enactment of temporary moratoriums on the hunting

restrictions wherever it is alleged to interfere with livestock operations. In order to better manage this species, its life history and local behavior patterns must be thoroughly understood. Although numerous reports have been published from various geographic areas concerning the Golden Eagle's productivity, nesting ecology, and behavior, little is known of its biology in Utah.

It was the principal objective of this study to determine the productivity, nesting ecology, and behavior of the Golden Eagle in west central Utah.

LITERATURE REVIEW

Gordon (1927) wrote one of the first thorough reviews of the nesting behavior of a pair of Golden Eagles in Scotland. Since that time much has been done to qualify and expand his findings. Watson (1957), Sandeman (1957), Lockie (1964), and Lockie and Ratcliffe (1964) have all added knowledge to the breeding activities of this species in various areas of Scotland.

Similarly, countless notes and articles have been published in the United States concerning various aspects of the Golden Eagle's ecology. Finley (1906) published one of the first of a long series of reports concerning the activities of this species in California. Slevin (1929) published an account concerning seven pairs of Golden Eagles over a six-year period in Santa Clara and San Benito Counties, California. Dixon's (1937) attempt to map the territories of various pairs of eagles has provided a record that has been substantiated by numerous accounts from several localities in North America.

With the exception of Cameron's work (1905, 1908) concerning some Golden Eagles in Montana, little information was published for the Rocky Mountain Region until the late 1940's. It was then realized that this region had one of the largest concentrations of Golden Eagles remaining in the continental United States. Many of the later reports (Wood, 1946; Williams and Matteson, 1947; Brown and Calley, 1950; Carnie, 1954; Fevold and Craighead, 1958; Strandtmann, 1962) were concerned with eye-witness accounts of various behavioral patterns or reports on the food habits of different populations of Golden Eagles. The latest effort to report life history data as well as detailed food habit information is that of McGahan (1967, 1968) concerning a population of eagles in southwestern Montana.

Unfortunately, only scattered reports (Tomney, 1942; Hardy, 1945; Hayward, 1967) on the status of the Golden Eagle in Utah have been published; it is anticipated that this study will begin to fill the void that exists in our knowledge.

LOCATION AND DESCRIPTION OF THE STUDY AREAS

The nest sites were grouped into two study areas which will be referred to as Area A and Area B. The principal study area (Area A) is located west of Utah Lake in Utah and Tooele Counties, Utah and contains approximately 540 square miles. It is bordered on the east by Utah Lake, on the north by a line running from Utah Lake to its intersection with

State Highway 36 on the west, south by a line running from Vernon to the extreme north front of the East Tintic Mountains, and east to Utah Lake. As indicated in Fig. 2, there are three broad land areas between the two parallel mountain ranges. These include (1) the lowland between Utah Lake and the Lake Mountains; (2) Cedar Valley west of the Lake Mountains; and (3) parts of Rush Valley west of the Oquirrh Mountains, Thorpe Hills, and East Tintic Mountains.

Area B includes several nest locations throughout west central Utah. Included are nests on the west front of the Wasatch Mountains near Provo in Utah County, Utah, as well as in several adjacent canyons. Other nests under observation are located in and around Yuba State Park, Juab County, Utah.

METHODS AND PROCEDURES

The study was conducted from January 1967 until July 1968 with the majority of the field work occurring during the nesting seasons (late February to early June) of both years. Field observations were made with the aid of a 20-power spotting telescope and a pair of 7x35mm field glasses; notes were taken on a portable tape recorder. Approximately 600 hours were spent in the field, which includes 150 nest visits.

Locating nest sites proved to be a demanding physical task which included observing the activities of adult Golden Eagles, thoroughly searching suspected nesting areas on foot, and taking two survey flights over the area. Additional information was obtained by consulting U. S. Fish and Wildlife Service personnel, through personal communication with John Hutchings of Lehi, Utah, and by reading the personal field notes of the late R. G. Bee of Provo, Utah; these two individuals are veteran field naturalists who compiled long-term records dealing with central Utah ornithology.

In order to obtain an accurate timetable of events, eyries were kept under observation during the stages of nest construction, incubation, and brooding. Burlap hides were placed near three eyries at the time of hatching to facilitate more detailed observations of the behavior associated with brooding and fledging. A photographic record of activity was taken with the aid of a 35mm single-lens reflex camera equipped with telephoto lenses.

Home range was determined by recording the direction of flight activity in relation to individual nests. The directions were then plotted on circle graphs as percentages, and these were placed around a map of the study area.

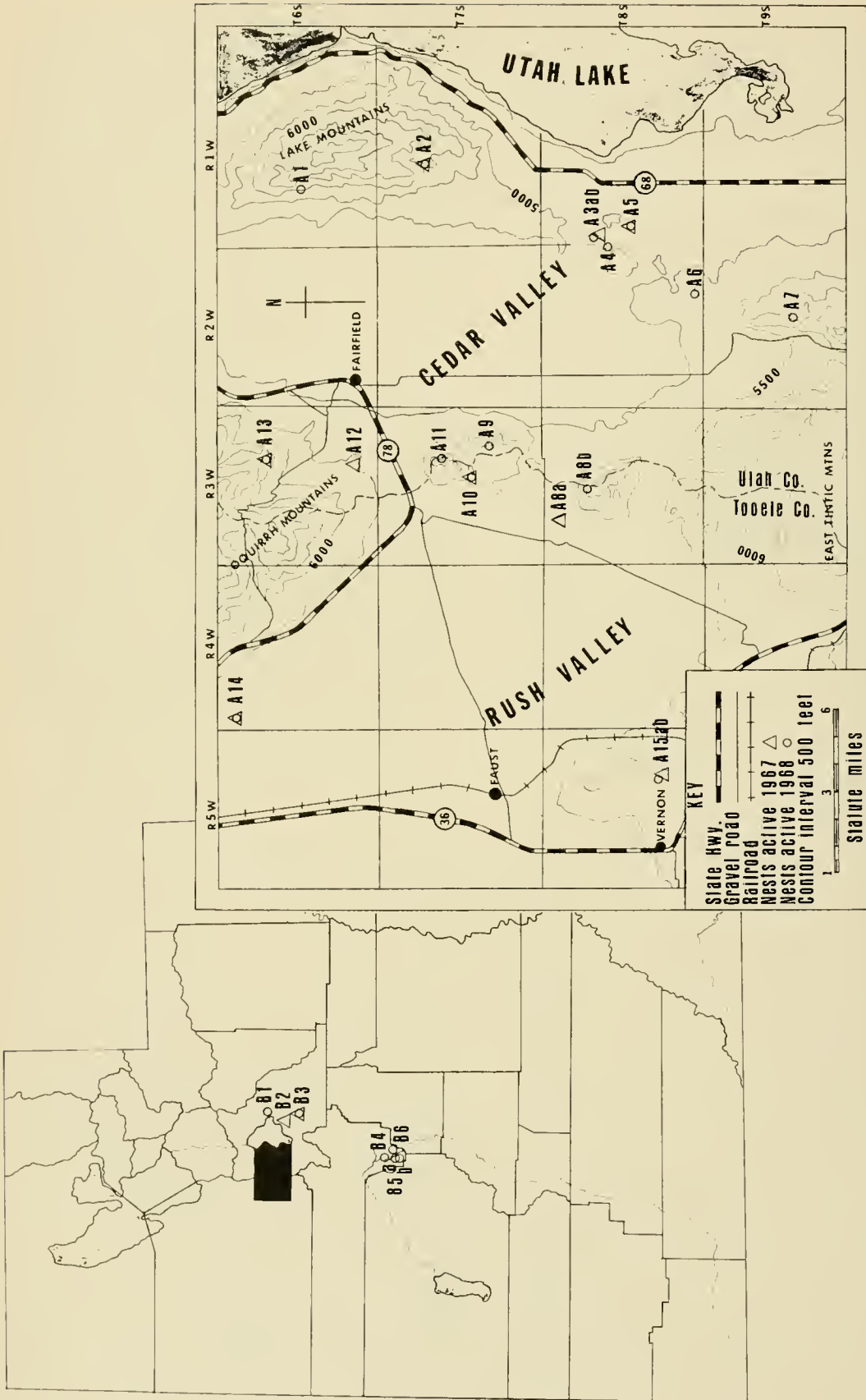


Fig. 2 Study Areas A and B.

Unsuccessful attempts were made throughout the winter of 1967-68 to live trap and mark Golden Eagles with the use of a Bal-chatri trap with both mammalian and avian bait. Victor No. 1½ and No. 2 spring jump traps with padded jaws were also placed on favored roosting posts in Cedar Valley. This resulted in the capture of two Great Horned Owls (*Bubo virginianus*), one Short-Eared Owl (*Asio flammeus*) and one Long-Eared Owl (*Asio otus*), but no eagles were obtained.

RESULTS

Nest locations. A total of 31 active nests¹ were observed during the two-year period. Of these, 11 were recorded in 1967 and 20 in 1968. The increase in 1968 was owing to the addition of the Yuba State Park area nests, as well as the discovery of additional nests in Areas A and B.

Eighty-seven percent of all nesting activity occurred on cliffs (27 activities), 6.5 percent (2 activities) on the ground and 6.5 percent (2 activities) on an artificial structure. The latter structure, located on the U. S. Army Deseret Depot Activity (Nest A-14), is an abandoned gunnery tower extending 11 meters above the ground. The nest is situated at the top and surrounded by a 1 meter high metal railing and a 2 meter high wooden frame (Fig. 3).

The ground nest (A-5) is located atop a rock ledge three meters high. The ledge remains level for about 1.5 meters, and then rises at an angle of approximately 13 degrees to the top of the hill.

All except five nests were reached without the aid of ropes. The nests ranged from two meters (A-4) to 13 meters (A-8) above the base of the cliffs. Most of these cliffs are limestone, with the exception of one (B-3) which is sandstone, and three others (B-4, B-5a and b, and B-6) which are shale.

Altitudinal distribution. Of all active nests in the study area, 61.3 percent were at altitudes between 5,000 and 6,000 feet, 9.7 percent below 5,000 feet, and 29.0 percent above 6,000 feet (Table 1). The altitudinal extremes are nests A-5 and A-13 at approximately 4,750 feet and 6,800 feet respectively, with the average altitude for all active nests being 5,750 feet.

Nest aspect. For both years, 55.5 percent of all active cliff nests faced west, 22.2 percent north, 18.6 percent south and 3.7 percent East (Table 2). There is no apparent difference either in the number of available cliffs facing various directions or in the distribution between



Fig. 3. Tower nest (A-14) located at U. S. Army Deseret Depot Activity, Tooele County, Utah (1968).

TABLE 1
Number and percentage of Golden Eagle nesting activities at various altitudes in Area A and B.

Altitude range (feet)	1967		1968		Total	
	No.	Percent	No.	Percent	No.	Percent
4,000-5,000	2	18.2	1	5.0	3	9.7
5,000-6,000	6	54.5	13	65.0	19	61.3
6,000-7,000	3	27.3	6	30.0	9	29.0
Totals	11	100.0	20	100.0	31	100.0

TABLE 2
Exposures of active cliff nests for Area A and B.

Direction of Exposure	1967		1968		Total	
	No.	Percent	No.	Percent	No.	Percent
North	3	33.3	3	16.7	6	22.2
East	0	0.0	1	5.5	1	3.7
West	4	44.5	11	61.1	15	55.5
South	2	22.2	3	16.7	5	18.6
Totals	9	100.0	18	100.0	27	100.0

the two years. This is in addition to the tower and the ground nests that were active both years and were completely exposed to all directions.

Nest size. The largest nest (A-3b) measured 1.0 meter wide, one meter from front to back,

¹Active nests are defined as those showing new decoration and/or the presence of adult birds during the nesting season.

and 1.6 meters high, and had a large amount of nesting materials on the ground immediately below. This was the only nest with an easterly exposure and was located on a small ledge half-way up on a 9 meter cliff. The smallest nest was believed to be A-1, but unfortunately, it was destroyed before accurate measurements could be taken. With the aid of photographs and measuring the debris, it was estimated to be one meter long, 0.7 meter from front to back, and 0.5 meter high. This nest was located on loose rock in a limestone quarry and collapsed, presumably under its own weight, when the Eaglets were ten days old.

Nest materials. Nest materials usually reflected the surrounding vegetation in both composition and abundance. Those nests with juniper or pinyon pine nearby had an abundance of shredded bark as lining, leafed branches as decoration, and larger branches in the main structure. Nest A-2a had as its lining both shredded juniper bark and juniper leaves in almost equal proportions. This is in contrast to A-6 which had predominately pinyon branches, leafed and about 0.3 meter long, not shredded into a fine mulch but packed with use.

Only nest A-3 had foreign material incorporated into the nest. It contained a piece of wire about two meters long placed vertically on the outside of the nest and extending slightly above the top edge.

NEST DENSITY AND HOME RANGE

Pair density. Pair density and all home range data were taken only from Area A which contained approximately 540 square miles of land area including villages and cultivated fields. In 1967, nine nesting pairs were recorded in the area, for an average density of one pair per 60 square miles. This is in contrast to 14 nesting pairs in 1968 averaging 38 square miles per pair. These figures express the maximum area per pair, for rarely during the nesting season were adult birds seen in the townships east of Faust in Rush Valley or east of Fairfield in Cedar Valley, and unknown nesting pairs may also have been present

The two active nests with the greatest unoccupied distance between them were A-15 and A-14, 16.1 miles apart. This area was occupied predominantly by sheep and cattle operations and provided virtually no nesting habitat for eagles. The closest active nests, 0.7 miles apart, were found in 1968 when A-3b and A-4 were both active. The divide between the two nests was 125 feet higher than A-3b and 225 feet high-

er than A-4. A third nest active in 1968 (A-5) completed a triangle whose sides measured: A-3b to A-4, 0.7 miles; A-4 to A-5, 1.5 miles; and A-5 to A-3b, 1.5 miles. The area of this triangle was 0.5 square miles.

Home range. Only in area A was an attempt made to measure home range. The direction of all eagles going to or from their nests was recorded and only those nests with four or more sightings appear in Fig. 4. Recordings for both years were included when the same nest or known alternate nests were involved.

The birds of nest A-15a and b and A-8a and b had their activity rather evenly distributed in four directions. Those of nest A-15a and b had 33.3 percent of their activity to both the north and south and 16.6 percent to both the east and the west; while A-8a and b had 18.2 percent to the east and the west, 36 percent to the south, and 27 percent to the north.

Pairs A-5, A-4, A-3, and A-2a and b had their activity somewhat restricted to various directions. The birds of nest A-2 had no sightings to the north while 37.5 percent were to both south and east, with 25 percent to the west. Pairs A-3, A-4, and A-5 had their activity primarily in opposite directions. Fifty-four percent of the activity of A-3a and b was to the north, while 45.5 percent and 31.8 percent of the activity of A-5 was to the east and south respectively. All of the activity of pair A-4 was evenly divided between both the south and west. Similarly, pairs A-9, A-10, and A-11 had the greater part of their activity in directions opposite to each other. Sixty-one percent of the activity of pair A-10 was to the south, while pair A-11 had 50 percent to the north and 33.3 percent to the east. Pair A-9 had 66.6 percent to the south and 33.3 percent to the east and no reported activity to the north and west.

Alternate nests. Many of the pairs of eagles had one or more alternate nests. Eleven of the 21 pairs considered had known alternate nests. Of these, 8 pairs had three nests and 3 pairs had two. Three of the 11 pairs with alternates are known to have used different nests the same year. The distance from active to alternate nests ranged from slightly less than 25 meters at A-4 to 1.3 miles at A-8.

NESTING ACTIVITY

Nest preparation. Preparation of the nests varied greatly, with several being almost doubled in size prior to nesting, while others remained virtually unchanged. Nest A-10 was increased in height nearly 0.4 meter for the

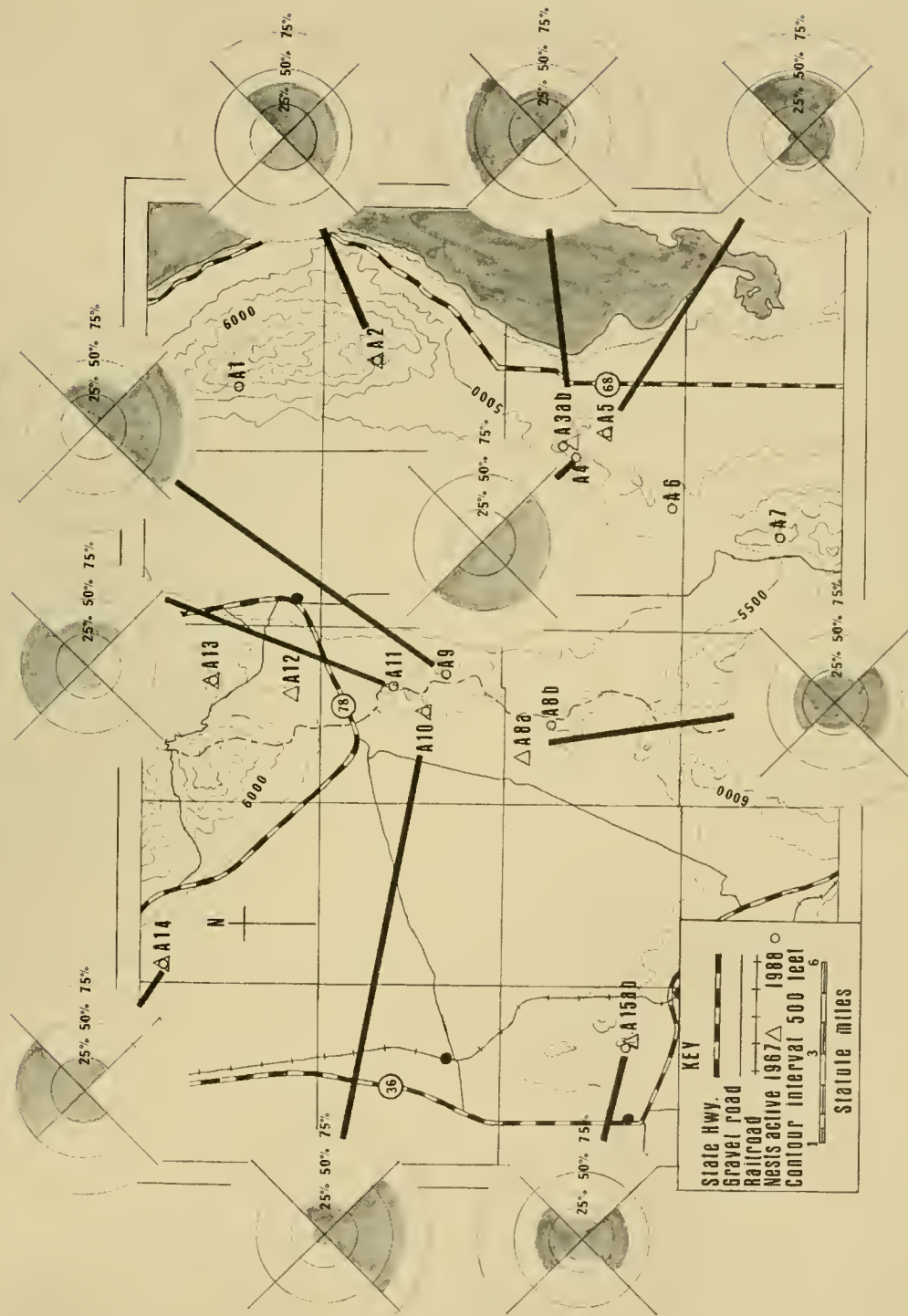


Fig. 4. Home range based on directional activity.

1968 season; in contrast, nest A-5 was enlarged very little during the same period. Of all the nests studied for the two years, 54.5 percent had an increase in height of 0.1 meter or more, while the remaining 45.5 percent had less than 0.1 meter of new material added.

Egg laying. Egg laying dates varied from year to year as well as within a given year. The first egg was noted in nest A-3b on February 25, in A-10 on February 26, and in A-14 on March 1, 1968. Two eggs were seen in nests B-5 and B-6 on the second of March, 1968, and in nest A-15 on the fourth of March, 1968. This is in contrast to 1967 when, based on a 42-day incubation period, the first eggs were laid on March 6 at nest A-10 and March 9 at Nest A-14. Two eggs were found in nest A-3a on March 11, 1967, but unfortunately no laying date could be determined, as the nest was destroyed before hatching.

The last two eggs laid in 1968 were found on April 11 at nest B-5b, and were abandoned about May 16, with evidence that incubation had lasted nearly 35 days. This is believed to be the second nesting effort for this pair, their first having ended with two abandoned eggs about March 17, 1968 at nest B-5a. Another late nesting date occurred at nest A-7 where one young hatched about May 5. Based on a 42-day incubation period, the egg would have been laid about March 24.

Temperature data from the two years indicate no appreciable differences and provide no obvious correlation between the laying dates for both years.

Incubation periods. Fairly accurate incubation periods were obtained from three nests. Nest A-15b had an egg present on March 4 and the young eaglet was estimated to have hatched between April 12 and 14. This would indicate a minimum of 39 to 41 days of incubation. However, it is believed that this egg was laid March 2 when the bird was observed for 35 minutes to be sitting on the nest. This would increase the incubation period to a probable 41 to 43 days. Similarly, nests A-14 and B-6 held two eggs each on March 1 and 3, respectively. The estimated dates of hatching are April 13 to 15 for the eggs of nest A-14 and April 14 to 16 for the eggs of nest B-6. This results in a minimum 41- to 43-day incubation period for both clutches.

Fledging. The length of time required for the young to fledge varied from 8.5 weeks to 10 weeks. Pair A-8b hatched two birds about April 7, shortly after which one died. Fifty-nine

days later, on June 5, the nest was empty, and what is believed to be the remaining bird was seen 1.5 miles east of the nest resting on a low ledge. It allowed our vehicle to approach within 100 meters, and then flew poorly for about 0.25 mile, and landed roughly on a hillside.

One young at nest A-15b fledged in approximately ten weeks in 1968, and two young fledged in 9 weeks in 1967. Three other pairs (A-5, A-12, and A-14) each fledged one bird in nine weeks in 1968, and pair A-4 fledged two birds in this same period in 1968.

PRODUCTIVITY

In 1967 and 1968, 23 nesting pairs of Golden Eagles produced eggs for an average of 1.91 eggs per nest. Three pairs produced one egg each, 19 produced two eggs each, and the remaining pair produced three eggs (Table 3). A total of 31 active pairs in 1967 and 1968 hatched 35 birds for an average of 1.13 young per pair. Twenty-six or 74 percent of these subsequently fledged for an average of 0.84 fledglings per pair for both years (Table 4).

Unsuccessful nests. Six of the 13 nesting attempts that failed are believed to have been interfered with by humans. Nest A-3a and b were destroyed during incubation in both years of study. In 1967 the female was shot off the nest by a small caliber bullet and both eggs destroyed, and in 1968 all three eggs were found broken in the same area below and to the side of the nest. Nests A-6, A-10, and A-11 had the eggs removed, and no remains could be found in or around the sites. Four people with a rope were seen near nest A-11 on the last day the eggs were reported present.

Human interference is also blamed for the abandonment of nest A-8a in 1967 before eggs were laid. It is known that at least one man attempted to approach this nest with a rope on the last day it was reported active.

One nest (A-2) was abandoned in 1967 after a fire of unknown origin destroyed a wood rat den 12 meters to the side of the nest. Although the nest and egg were undamaged they were

TABLE 3
Clutch size for various Golden Eagle nests for Areas A and B

Clutch Size	1967		1968		Total	
	No.	Percent	No.	Percent	No.	Percent
1	1	14.2	2	12.5	3	13.0
2	6	85.8	13	81.3	19	82.6
3			1	6.2	1	4.4
Total	7	100.0	16	100.0	23	100.0

TABLE 4
Productivity records, 1967-1968, Areas A and B

	Area A	Area B	Area A and B
Number of nesting efforts 1967	9	2	11
Number of nesting efforts 1968	14	6	20
Number of nesting efforts with eggs 1967	7	1	8
Number of nesting efforts with eggs 1968	13	6	19
Number hatched 1967	10	2	12
Number hatched 1968	17	6	23
Average number hatched per nest 1967	1.11	1.00	1.09
Average number hatched per nest 1968	1.21	1.00	1.15
Average number hatched per nest 1967-68	1.17	1.00	1.13
Number fledged 1967	7	2	9
Number fledged 1968	12	5	17
Average number fledged per nest 1967	0.78	1.00	0.82
Average number fledged per nest 1968	0.86	0.83	0.85
Average number fledged per nest 1967-68	0.83	0.88	0.84
Percent of hatched that fledged 1967	70.0	100.0	75.0
Percent of hatched that fledged 1968	70.5	83.3	73.9
Percent of hatched that fledged 1967-68	70.3	87.7	74.3

abandoned, even though the eagles remained in the area. The cause for abandonment of this nest in 1968 was never determined.

As mentioned previously, nest A-12 collapsed in 1967 causing the death of both young.

Nest B-5a was abandoned with two eggs at least 14 days after incubation started. Possible explanations include the placement of a hide near by, or the constant activity of approximately 12 starlings in and around the structure of the eagle nest. Approximately 25 days after the initial abandonment, two eggs were noted in nest B-5b, 0.7 mile south of the first nest. This clutch was abandoned nearly five weeks later for no apparent reason.

Only the pairs at nests A-5 and B-2 in 1967 failed to produce eggs, although they remained in the area for most of the season.

BEHAVIOR

Incubation. Most of the incubation was done by the female. The only observed exceptions to this occurred on three occasions at two different nests when the male was seen to alight on the nest in mid-afternoon and to relieve his mate. This appeared to last less than two hours, at which time the male left the nest before his mate returned.

Nest sanitation. The nests were kept free of food remains during the incubation period by the adults who carried the debris away. However, this was not the case once the young hatched. Food remains built up to a point where

at nest A-8b parts of 12 jackrabbits were on the nest proper. Nest A-14 had much the same situation from the time the young was four weeks old until it fledged.

Alternate roosts. The male spent very little time at the nest. Of all the nest visits, there were only two occasions when it was certain that the male and not the female was on the nest. In several cases there were roosting sites near the nest where the male spent much of his time. Site A-3b had such a roost 15 meters above and to the south of the nest. Birds of nest A-4 used the large hill directly south of the nest, and an alternate nest 30 meters to the east. Nest A-5a had two roosting locations, one 110 meters to the northwest on a higher ledge, and another approximately 0.25 miles west of the nest. Other obvious roosts occurred at nests B-4 and B-6, immediately above and to the east of the nest and to the south of the nest respectively.

Nest aspect. Nest A-5 was exposed in all directions to the sun, and the young appeared to suffer from the heat. The female of this nest was often seen shading the young with her wings. On four occasions the male brought large tumbleweeds to the nest; three times he placed them to the west side of the nest where they provided some shade for the young. The young spent much time in gular panting, with its legs and wings outstretched on the nest.

On two occasions at nest A-4, the young were seen to seek the small available areas of shade to the extent that they crowded each other and

forced the smaller bird to occupy an exposed position.

Nest Defense. Only three of the nesting pairs showed any indication of defensive behavior. Most of the birds would fly out of sight as soon as they were aware of my approach. One exception was the pair at nest A-5. From incubation to fledging, these adults would stay in the area when disturbed and at time call in a rather shrill "cherop" sound. Particularly during incubation the female would remain within 45 meters and circle and call while the male, if present, would be higher and usually silent. This type of behavior continued through the fledging period with only the call being omitted. At this nest the young began leaving the nest and walking about on the hillside when 6.5 weeks old, and on at least one occasion before the young fledged, the female came to within 50 meters of me, circling and calling. Although this bird made no aggressive moves when disturbed, she did remain nearby and defensive. All defensive activity decreased sharply if two or more persons visited the nest at the same time.

The female at nest B-5 would not leave the nest until observers were almost within touching distance; when she occupied nest B-5a, I could approach to within 10 meters of her, and later when at nest B-5b, this same female would not leave until someone was looking over the edge of the nest. Upon leaving she usually circled two or three times in the immediate vicinity before disappearing.

The third eagle to show any indication of defensive behavior was at nest A-12 during the 1967 nesting season. On one occasion, I was able to approach to within 25 meters in a vehicle and then subsequently climb to the nest while in full view of the bird and touch her wing. She left, however, when the nest was reapproached to within two meters from above. At this time there were two one-week old eaglets in the nest.

Fledging behavior. Prior to leaving the nest, the eaglets appeared to perform wing exercises. This was noted on several occasions at nests A-5, A-15, and B-3. The eaglets started stretching their wings over their backs when five weeks old and progressed to wing flapping until their first flight. The eaglet of nest A-5 left the nest when 6.5 weeks old and two weeks later was seen walking on the hillside with a combination of wing flaps and jumps. When approached, this bird attempted to fly down the hill but was unable to get off the ground for more than short

wing jumps. The following day under similar conditions, this bird did manage to fly about 200 meters down the hill with a combination of glides and stiff wing flaps. Once on the level valley floor it was unable to regain flight and was then captured and carried to the top of the hill and released.

The first flight of the eaglet in nest A-11 was one of little hesitation. When approached from above, it walked to the nest edge and immediately jumped off and with a series of very stiff wing and tail flaps it glided 250 meters to the valley floor. Once there it also could not regain flight and was captured after attempting to defend itself by lying on its back and extending its open talons. This bird was also returned to the hilltop and released.

The eaglets of nest A-15 in 1967 and A-4 in 1968 had very similar initial flights. Only the last eaglet to leave nest A-15 was observed as it jumped off the nest after making two approaches to the edge. It glided at least 350 meters with no real wing flapping and only the most abrupt turning. When about halfway into its flight, it produced two very plaintive "cherops" and continued to its destination, a juniper tree.

Both young in nest A-4 left the nest at about 7.5 weeks and were found on another ledge 20 meters above and to the northwest of their nest. These birds apparently walked slowly to this point, possibly taking several days, as droppings could be seen leading from their nest to this final roosting area. These birds both jumped off this ledge and glided, one to the west 300 meters and the other southeast 500 meters, before landing in low sagebrush.

The first flights of all these young, with the exception of those of nest A-11, were witnessed by at least one of the adult birds. Only nest A-8b contained large amounts of food after the young had left. At none of the other nest sites was there any food found, although all had remains scattered about. No adults were seen near the young before their flight, and adults made no attempts to come to their aid during the flight.

Renesting attempts. There were two cases of renesting attempts after the failure of the first nest. In 1967 nest A-2 was abandoned after a fire destroyed a nearby wood rat den. Three weeks later both eagles were seen carrying sticks to an alternate nest site 150 meters southwest of the original nest. Examination of this site indicated that material had been added to a height of 0.8 meter above the existing structure in the form of a pyramid. Later examina-

tion indicated that nest construction had ended at this stage.

Nest B-5a was abandoned with two eggs about March 17, 1968, and six days later on March 23, new decorations were evident on an alternate nest 0.7 miles south of the first. On April 11 two eggs were reported in this new nest, only to be abandoned between May 12 and 16. Examination of these last two eggs revealed feathered embryos with well-developed claws and bills. This would indicate that incubation had lasted at least 30 to 35 days, and that the eggs were laid about April 10 or 11. This allowed a period of 24 days from the time of the first nest abandonment to the time the second set of eggs were laid.

DISCUSSION

NEST LOCATIONS

The distinctive topographic features of Area A are the parallel mountain ranges with broad open valleys on either side. These mountain ranges provide an abundance of cliffs for potential nest sites, while the valleys with their rodent and lagomorph populations furnish excellent hunting areas. This undoubtedly accounted for the fact that of the 31 nesting activities reported in the two years, 87 percent occurred on cliffs, 6.5 percent on the ground, and 6.5 percent on an artificial structure. There were few trees large enough for nest sites in area A or around nests of Area B.

The utilization of the gunnery tower at site A-14 had enabled this pair of eagles to use this otherwise unsuitable portion of Rush Valley as their hunting range. The closest natural nest site would be in the Oquirrh Mountains five miles to the east or on the ground on several low hills. This location in the U. S. Army Desert Depot Activity offered protection from human hunting pressures and an abundant jack-rabbit population.

The ground nest at A-5 is believed to be an abandoned Ferruginous Hawk (*Buteo regalis*) nest. Both McGahan (1968) and Wellein and Ray (1964) have reported unoccupied eagle nests on the ground.

McGahan (1968) reported that about 71 percent of the active nests in his study in southwestern Montana were on cliffs, with the remainder in trees. Wellein and Ray (1964) reported that of the 79 occupied and unoccupied nests found in Texas and New Mexico, 87 percent were on cliffs, 11 percent in trees, and one nest was on the ground. Only Murie (1944) had no tree nests to report when he observed 23 nests,

all on cliffs, in Alaska. Bee (unpublished field notes) reported an active eagle nest in a fir tree on the eastern slope of the Lake Mountains of Area A in 1936. This nest could not be located in the present study.

The altitude of the active nests reflected the surrounding topography. The average altitude for all active nests in the study was 5,750 feet, with no nesting activity seen above 6,800 feet. Sixty-one percent of all active nests were located between 5,000 and 6,000 feet with 9.7 percent below 5,000 feet and 29 percent above 6,000 feet. A probable explanation is that only limited hunting is possible in areas at altitudes above 6,500 feet. McGahan (1968) has suggested that nest site preference is influenced by the direction of the sun's rays; he reported that 49 percent of the nests in his study faced south, 14 percent west, and 23 percent east. Twenty-two percent of the active nests in my study faced north, 56 percent faced west, and 19 percent south. These figures fail to provide any evidence for or against the effect of the sun as a determining factor in nest selection.

NEST DENSITY AND HOME RANGE

Pair density and home range were determined for Area A only. The nine nesting activities reported in 1967 averaged 60 square miles per pair. With the addition of five more nests in 1968, the average dropped to 38 square miles per pair. This figure indicates a maximum area per pair, because few adult eagles were reported in areas near Faust in Rush Valley and Fairfield in Cedar Valley.

This density seems to coincide with reports from other areas. Dixon (1937) found that the 27 pairs observed in Southern California averaged 36 square miles per pair. Arnold (1954) in his study in Colorado found six pairs occupying six adjacent townships, and Lockie (1964) reported that his Scottish eagles averaged 27.1 square miles per pair. Another Scottish eagle study (Watson, 1957) indicated that five pairs of eagles averaged nine square miles of territory. McGahan (1968) found the birds in his study to average one pair per 66.3 square miles.

The shortest distance between active nests was 0.7 miles. A nearby nest provided the third point in a triangle the area of which was 0.5 square miles. McGahan (1968) reported two active nests being 1.0 mile apart but left it unclear as to the topography and home range allotment between the nests. Dixon (1937) stated that nesting pairs are sometimes within two square miles.

On a basis of the information concerning direction of activity of the various eagle pairs, their home ranges generally appeared to be opposite each other. Pair A-3a had 54.5 percent of their activity to the north and 27.3 percent and 18.2 percent to the east and south, respectively. By way of contrast, the activity of pair A-4 was evenly distributed between west and south. Pair A-5 had 45.5 percent and 31.8 percent to the east and south respectively, with only 18.2 percent to the west. This activity to the west was centered toward the roost located 0.25 mile in that direction, and at no time was there an indication of any bird of nest A-5 going far beyond this point. These birds were often seen hunting the area between their nest and the lake. It appears that these three nests are at the apex of their home ranges and that these ranges radiate away from each other. This corresponds to Dixon's (1937) statement that eagles have their nests on the margin of their hunting range, and their activity radiates away from each other.

A similar situation appears to exist with nests A-9, A-10, A-11, and A-14. The direction of their activities indicates that their proximity to each other is only on the basis of nest site, and does not indicate an overlapping of ranges. Considering the lack of adequate nest sites in the valleys, this is the most effective way to utilize the available hunting area.

The birds of nest A-14 had most of their activity directed toward the north away from the Deseret Depot Activity. Those of nests A-8a and b and A-15 had their activity distributed in all directions, with slightly more to the north and south. This corresponds to the isolation of the respective hills and the somewhat north-south oriented highlands around their nests. Particularly at nest A-14, the adults were never seen low over the valley floor but always along the open ridge tops extending both north and south. It appears, therefore, that these nests are located near the center of the eagles' ranges.

NESTING ACTIVITY

Earliest egg laying dates for both years differed by at least 10 days, from 24 February in 1968 to 6 March in 1967. There appears to be no correlation between this difference and the temperature variation between those two years. The average high temperature for January of both years was essentially the same, while the average low temperature for January 1967 was 5.2 degrees F. higher than for the same period in 1968. The high temperatures for February

1968 averaged 3.2 degrees F. higher than for the same period in 1967, and the low temperature for February 1968 averaged 4.4 degrees F. higher than for the same period in 1967. It is doubtful that these temperature differences account for the difference in egg-laying dates.

The incubation rate for the eagles in this study was determined to be 42 days. This corresponds closely to the 45 days determined by Hobbie and Cade (1962) in their work on some Alaskan eagles but is somewhat above the 33 to 35 days listed by Carnie (1954) for his study in Santa Clara County, California. Walker and Walker (1939) reported that a single nest in Southern California had a 43-day incubation period. Bent (1938) lists 28 to 35 days as the incubation time but adds that 35 seems more correct.

The male was seen to assist during incubation by relieving his mate in the afternoons. Walker and Walker (1939) also found this to be the case with one pair of eagles in Southern California. They stated that the male incubated from noon until 4 p.m., while the female rested. The male spent much of his time hunting or sitting on nearby roosts.

Summer (1929b) and Carnie (1954) both stated that the young remain in the nest from 65 to 70 days. Seventy-five days is the length of time Hobbie and Cade (1962) reported as required for fledging. In the present study, fledging periods varied from 59 to 70 days. The nest with a 59-day fledging period had only one young for the last seven weeks, and this bird was always supplied with more food than was eaten. This would indicate that the young are not starved from their nests but leave for other reasons as yet unknown.

The combined data for 1967 and 1968 resulted in 23 nesting pairs producing 44 eggs for an average of 1.91 eggs. This is only slightly lower than the 2.1 eggs per nesting pair reported by McGahan (1968). However, 1.13 eggs per pair hatched over the same period as compared to 1.8 and 1.59 respectively reported by McGahan (1968) and Wellein *et al* (1964).

A total of 26 eagles fledged for an average of 0.84 fledglings per nesting pair. This is considerably less than the 1.37 and 1.32 fledglings per pair stated by McGahan (1968) and Wellein *et al* (1964) but is similar to that described by Watson (1957) who found 0.8 fledglings per pair in Scotland.

The two reported renesting efforts (A-2, 1967; B-5a and b) seem to coincide with reports by Hanna (1930) and Dixon (1937) who es-

tablished 30 days and 28 days respectively between sets of eggs. Twenty-one days after nest A-2 was abandoned, the adults were seen carrying nesting materials to the new site. Although no eggs were laid in this second nest, the time interval would appear to coincide with a 28-day schedule.

Nest B-5a was abandoned on April 11, and 25 days later 2 eggs were seen in nest B-5b. It is believed that this was the same female. Her mottled color and willingness to stay on the nest when approached were the principle evidences for this belief.

SUMMARY

This study consisted of two years of observation on a population of Golden Eagles (*Aquila chrysaetos canadensis*) in and around Utah and Tooele Counties, Utah. The area can be classified as part of the sagebrush-shadscale biome with some juniper and pinyon pine growing on the higher ground. The topography of the major study area consisted of two parallel mountain ranges separated by broad open valleys.

Thirty-one nesting activities were observed over the two-year period. Of these, 87 percent were on cliffs, 6.5 percent on the ground, and 6.5 percent on an abandoned gunnery tower at the Deseret Army Depot in Tooele County, Utah.

The average elevation for the cliff nests was set at 5,750 feet with no nesting activities seen above 6,800 feet. Fifty-five percent of all active cliff nests faced west, 22 percent north, 19 percent south, and 4 percent east.

The size of the nests varied from the largest measuring 1.1 meters wide, 1 meter from front to back, and 1.6 meters high to the smallest measuring 1 meter wide, 0.7 meter from front to back, and 0.5 meter high. The materials used in nest construction reflected the surrounding vegetation in both composition and abundance.

Pair density and home range were determined for the 15 nesting activities in the major study area only. The greatest unoccupied distance between active nests was 16.1 miles, and the shortest distance between active nests was

0.68 miles. Pair density was set at one pair per 60 square miles in 1967, and one pair per 38 square miles in 1968. Three active nests were noted that formed a triangle whose area was 0.48 square miles.

Home range was based on the direction of activity of the adult birds from their nests. Eight nesting pairs were determined to have their nests on the perimeter of their ranges, while two other pairs located their nests near the center of their activity.

The first eggs reported for both years were laid on or about March 6, 1967, and February 24, 1968. The incubation period was determined to be 42 days, with the male assisting for only a limited amount of time during the afternoons. Fledging periods ranged from 59 to 70 days.

Productivity was broken down in the following manner: 11 nesting efforts in 1967 yielded 12 hatched young, and 9 of these fledged for an average of 0.82 fledglings per nesting effort, as compared to 20 efforts in 1968 with 23 young hatching and 17 eventually fledging, for an average of 0.85 fledglings per nesting effort. Seventy-five percent of the hatched birds fledged in 1967 as compared to 74 percent in 1968.

Adult defensive behavior was noted at three nests although no aggressiveness was apparent. It was noted in two cases that both young of a nest sparred for occupation of the shaded areas, with the smaller bird in both cases apparently forced to stay in the hot sun. This was in contrast to the situation at the one ground nest which was exposed to the sun at all times. Here the female was observed on several occasions partially spreading her wings and allowing the young to rest in her shade. On three occasions her mate brought tumbleweeds to the nest in an apparent attempt to shade the young eaglet.

Two renesting attempts were observed during the study. In 1967 a nest with one egg was abandoned, and the adults were seen adding materials to an alternate nest although they failed to lay eggs. In 1968, however, a nest was abandoned with two eggs, and the adults moved 0.7 mile and laid two eggs in a new nest. These, too, were abandoned before hatching.

NESTING ECOLOGY OF THE GREAT HORNED OWL *BUBO VIRGINIANUS*

by
Dwight G. Smith

INTRODUCTION

The Great Horned Owl, *Bubo virginianus*, is a common nocturnal raptor of North and South America, occurring in most habitat types. Although it presumably exerts considerable predatory influence on certain mammalian and avian populations, relatively little is known of its natural history and ecology owing to its secretive habits and the inaccessability of its nesting sites. Further interest is warranted in this raptor because of its decreasing numbers caused by a combination of factors, including habitat disruption owing to encroaching civilization, road kills, and indiscriminate shooting by hunters.

This study deals with the nesting ecology of the Great Horned Owl in the Great Basin deserts of central western Utah. Major aspects include nesting population and distribution, territoriality, and predation.

There are few comprehensive studies on the ecology of this species, and there appear to be no previous detailed investigations made in arid or semiarid habitats. Included among the more noteworthy studies are Baumgartner's (1938) work on its distribution and territoriality in New York forests, Errington's (1932) behavioral and predation studies in the cottonwoods of Wisconsin and the midwest, Orian's and Kuhlman's (1956) population and distribution study, also in the Wisconsin area, and Fitch's (1940, 1947) population and predation studies in the California chaparral. Utah literature on this species is limited but includes notes on its nest site selection (Sugden, 1928), breeding records (Bee and Hutchings, 1942), some life history and ecology data (Bee, unpublished data), a trapping note reported by Stanford (1931), and numerous local distributional records as exemplified by Hayward's (1967) *Birds of the Upper Colorado River Basin*.

METHODS AND PROCEDURES

STUDY AREA

The study locale of the first (1967) nesting season was the Thorpe Hills of central western Utah, an area of approximately 12 square miles of elevated topography located in Tooele and Utah counties (see Fig. 5). In the second study season (1968), the area was enlarged to include

the adjacent Toppliff Hills which increased the study area to approximately 25 square miles. These hills are low-lying extensions of the Tintic Range, with their highest elevations rising to about 1000 feet above the surrounding valley floors of Cedar and Rush Valleys.

FIELD STUDIES

The field work for this study was conducted for a period of two nesting seasons, the spring of 1967 and the spring of 1968. Field observations were aided by the use of 7 by 50 power binoculars and a 20 power spotting telescope.

Nests on the study area were located by a systematic search of all potential sites, that is, all cliff lines, rock outcroppings, abandoned quarries, and wooded areas. Those nests found were then plotted on a master map to determine the relative nesting population and distribution of the owls. Gaps in the suspected distribution were then rechecked several times during the nesting season for signs of roosting birds or nests previously missed. It was believed that all nests active during a given season were discovered and that an accurate picture of the nesting population and distribution of the Great Horned Owl was established during the two nesting seasons of the study.

Territorial studies were conducted at three nests, each representative of a different topographic site. These included a west-facing quarry nest and two cliff nests, one of which was located in an east-opening canyon and the other situated on a plateau with a western exposure. Territorial behavior was determined by visual observations during the hours from sunset until dark and was conducted from constructed blinds. Additional information on bird movements was gained from the plotting of sighting occurrences during the night. Owl movements were plotted, then territory size determined by planimeter measurements of the polygon formed by connection of points denoting the extreme distances from the nest site, following the method discussed by Odum and Kuenzler (1955).

Owl predation was determined by (1) weekly nest visitations to record prey types and frequency, and (2) pellet analysis.



Fig. 5. Study area location and vegetation

On discovery of a nest site, egg productivity was checked and the nest placed under weekly observation to note adult habits and egg-pipping time. After the young hatched the nest was inspected more frequently to ascertain food procurement items and adult territorial behavior. At nest abandonment with the development of flight by the young, nest measurements were taken and the remaining food items recorded and pellets removed for analysis. Data taken included nest size and material composition, its height relative to cliff size, and its elevation.

Additional data gathered included information on interspecific relations as determined by a search and location of active predatory bird nests in the vicinity of the owl nest sites.

RESULTS

NESTING POPULATION AND DISTRIBUTION

Fourteen nests were found on the study area during the 2 breeding seasons, including 4 during the 1967 season and 10 the following year on the enlarged study area (Fig. 6). Horned Owl population density on the study averaged .35

nesting pairs per square mile during the 2 study years. During this period 5 additional nests were found outside the study area but in similar habitat type; unless otherwise noted, all observations and tabular information pertain to the study area nests.

NESTS AND NEST SITE

Nest site and nest dimension data are presented in Tables 5 and 6. All four of the 1967 season nest sites were used the following year, thus 10 different sites were located during the two-year study. Birds on the study area utilized cliffs, abandoned quarries, caves and junipers for nest sites. Favored sites were large sandstone or limestone cliff faces or rock outcroppings. Three sites were deep in canyons, one on a plateau, and the remainder in the hills and foothills. Six of the nests were on western exposures, three faced south, and one had an eastern exposure. Site elevations ranged from 5300 to 5750 feet and averaged 285 feet above the valley floors. None of the nests were actually built by the owls, but eggs were deposited in old Raven, Redtailed Hawk, and Ferruginous Hawk nests appropriated

TABLE 5
Nest site selection of the Great Horned Owl

Nest number	Location	Site	Elevation	Valley floor elevation	Difference
1	Foothills	Old Ferruginous Hawk nest in 13' juniper	5550	5350	200
2	Quarry	Niche in 34' sandstone face	5750	5350	400
3	Quarry	Ledge in 18' limestone block	5650	5250	400
4	Quarry	Niche in 36' sandstone face	5300	5150	150
5	Quarry	Old Red-tailed Hawk nest in 67' shale face	5400	5400	0
6	Canyon	Old Raven nest in 29' limestone cliff niche	5650	5350	300
7	Canyon	Old Raven nest in 22' limestone cliff ledge	5450	5000	450
8	Canyon	Cave ledge in 38' limestone cliff	5750	5500	250
9	Plateau	Old Raven nest in 27' limestone cliff niche	5650	5300	350
10	Hills	Niche in 28' limestone cliff	5800	5450	350
Means			5595	5310	285

TABLE 6
Nest dimensions of the Great Horned Owl

Nest number	Height above ground	Crevice size*			Nest size*			Nest composition
		length	height	depth	length	width	thickness	
1	11'				28"	20"	14"	Juniper and sagebrush
2	14'	22"	40"	72"				Rock base litter
3	15'	16"	20"	15"				Rock base litter
4	13'	47"	36"	85"				Rock base litter
5	55'	38"	26"	18"	33"	18"	4"	Juniper and sagebrush
6	25'	30"	33"	60"	30"	60"	16"	Juniper and sagebrush
7	14'	25"	23"	65"	23"	23"	11"	Juniper and sagebrush
8	16'	204"	66"	156"	27"	27"	1"	Ground base litter
9	12'	28"	33"	42"	28"	35"	16"	Juniper and sagebrush
10	24'	41"	17"	32"	25"	19"	4"	Juniper and sagebrush

*where applicable

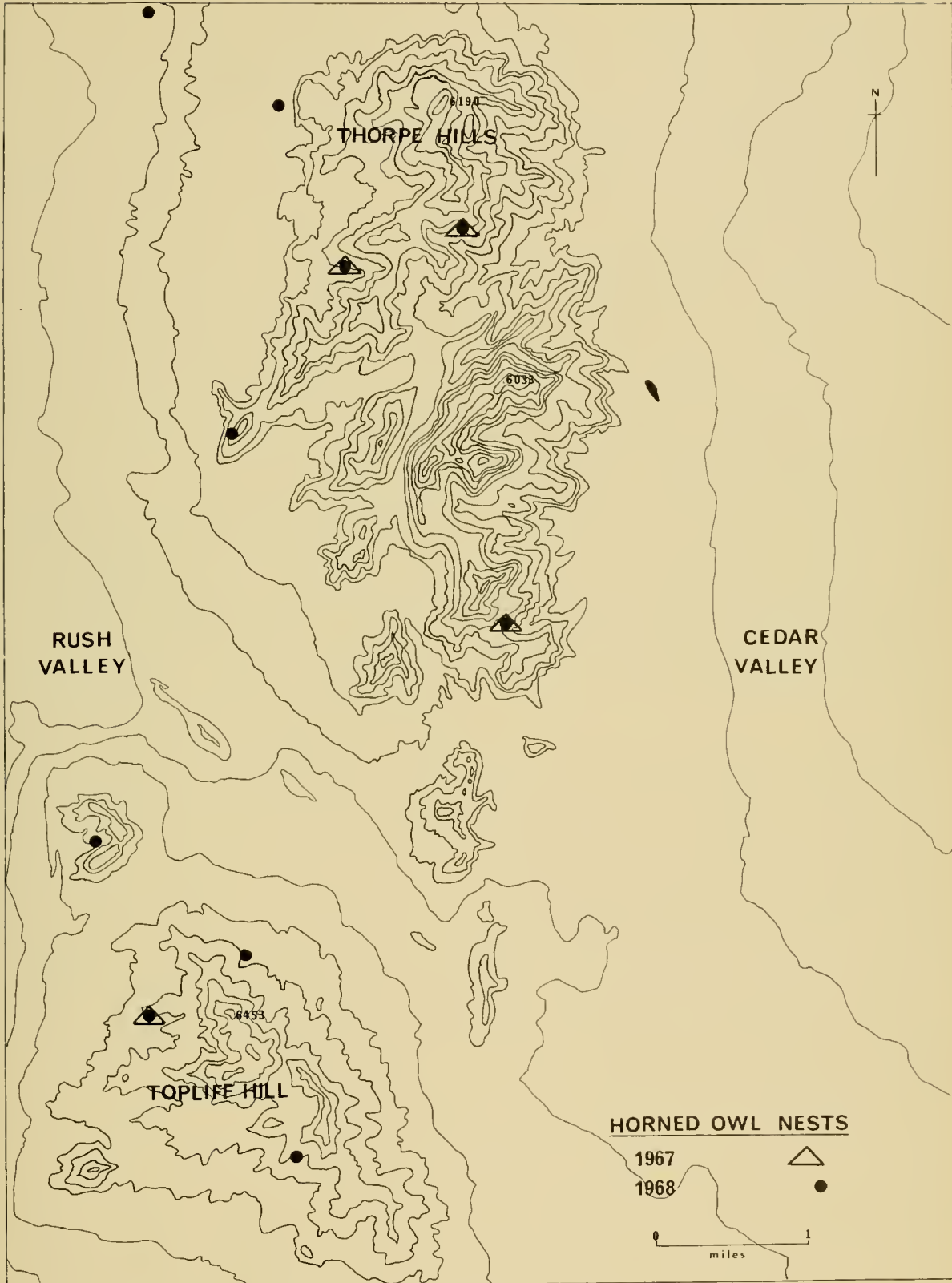


Fig. 6. Nest locations of the Great Horned Owl

by the early nesting owls, or were laid directly on unmodified rock or ground. Of the 10 nests, 4 were old Raven nests located in cliff crevices, one a Redtailed Hawk nest in a quarry crevice, one Ferruginous Hawk nest in a juniper tree, and the remaining 4 were on quarry and cave ledges. The nests outside the study area conformed to this pattern with the exception that one was located in a large Red-tailed Hawk nest high in a cottonwood tree.

The height of nests ranged from 11 to 55 feet above ground level. Nest size varied in proportion to crevice size, and as most nests were in poor repair, their external structure spilled throughout the crevice, conforming to the size and shape of the crevice. The larger nests actually formed the floors of huge cracks in the vertical stone faces of quarries, while the smallest nests were one ledge sites. Nests were composed of juniper and sagebrush twigs of varying sizes. All nests had extensive litter accumulation in the form of fecal material and prey and pellet remains. Toward the end of the nesting season this accumulation often spilled over the nests' edge forming large white streaks on the cliff face. Actual nest structure depended on 3 factors: age, exposure, and the original avian builder. The partially protected Raven nests tended to hold up best; they may thus provide several years of service.

NEST DISTRIBUTION

Nests were evenly distributed in the study area, with sites averaging one mile apart. Maximum and minimum distances between nearest neighbors for both nesting seasons were three miles and three-quarters of a mile. The closest sites were on opposite sides of the same mountain range, hence the nesting birds hunted in separate valleys. The extreme distance between successive sites occurred in an area of fewer potential nest sites, and supported lesser numbers of predatory birds for any species. All nests were located in the periphery of the hills on sites overlooking the deserts. No nests were found in the study area interior (see Fig. 6) although potential sites were available.

PRODUCTIVITY AND NESTING SUCCESS

A mid-September visit to the nests of the previous year (1967 season) disclosed no adult birds in the vicinity, but on December 2, (1967) I found a male occupying its nest site, presumably of the previous year. Owl pairs were initially observed together on January 5, and again on January 16, of the second study year. Egg-laying dates were between March 20 and April 10, in 1967, and between January 20 and February 10 in 1968.

In 1967 the 4 nests contained 8 eggs for an average clutch of 2.0 eggs per nest. In 1968 8 nests contained 24 eggs for an average clutch size of 3.0 eggs per nest. Maximum clutch size for the two-year study was 4 eggs while the minimum clutch size was one egg. In every case, repeat nests of the 1968 season contained one more egg than was contained in the 1967 season (see Table 7).

The fourteen nests of the 2-year study period hatched 29 young (2.1 per nest) and of these 23 (1.7 per nest) fledged, but yearly success varied. In the 1967 season, all nesting efforts were successful, but 5 of the 1968 study nests failed. Reasons for failure were ascribed to several causes based on circumstantial evidence. In at least 2 cases nest failure was attributed to human interference. Both nests failed after the young had hatched and survived for a period of 2 weeks. A third failure was attributed to interspecific action between close nesting Horned Owls and Red-tailed Hawks. In this case both species abandoned their nests after eggs had been deposited and were under incubation. Causes of the other 2 nest failures are unknown.

ADULT NESTING BEHAVIOR

The 2 sexes differed in nest habits. During the daylight hours males generally roosted in favorite secretive spots such as trees, unoccupied nests or nesting crevices, and ledges at distances from 5 to 250 yards from the nest site.

Females roosted in the nest during the day, taking flight only when alarmed. Typical female diurnal activity after the young hatched

TABLE 7
Nesting success of the Great Horned Owl

Year	Number of nests	Failures	Young per nest				Average clutch	Young hatched	Percent hatched	Young fledged	Percent fledged
			1	2	3	4					
1967	4	0	1	2	1	0	2.0	8	100	8	100
1968	10	5	0	1	6	1*	3.0	21	88	15	63

*Two histories unknown because of early nest failures.

consisted of positioning herself between the young and the edge of the nest. In this stance she would doze, occasionally awakening to visually sweep the nest site environs. The female would usually leave the nest approximately 45 minutes after sunset regardless of weather conditions, and join her mate at the roost, after which the pair would begin their nocturnal activities.

NEST DEFENSE

Nest defense behavior differed with respect to sexes. Males took flight readily, but females remained on the nest until I flushed them. Six nesting pairs simply disappeared after being alarmed, but females of three nests would hoot protests from concealment. The female at nest ten repeatedly carried out determined attacks against me when I was near the nest.

TERRITORIALITY

Territories of 3 nesting pairs were determined during the growth of the young and are presented in Figure 7. Both hunting activity and sighting locations were plotted, thus maximum territory was established (Odum and Kuenzler, 1955). Results indicate territorial sizes of 172, 237 and 376 acres for the nests, or an average territory coverage of 261.6 acres. Territory size varied with topography. The largest territory (Fig. 7; nest 9) had the nest site on a plateau, and the nesting birds hunted in both surrounding valleys. The smallest determined territory (Fig. 7; nest 6) had its site in a narrow canyon with owls extending their hunting activity along a narrow strip into the desert. All determined territories extended only slightly into mountains but ranged far into the desert valleys. In no case did the size of the feeding territory have a radius exceeding one-fourth mile from the nest site into the hills, but the radius extending into the deserts ranged from one mile to one and one sixth miles, and spot observations on a fourth nest indicate a possible territorial range of two miles into the valleys.

INTRA AND INTERSPECIFIC RELATIONS

No interactions were observed between nesting pairs of Horned Owls, and no other large owls occurred in the study area. The medium sized Long-eared Owl (*Asio otus*) and Short-eared Owl (*Asio flammeus*) occur in the surrounding valleys, but neither species was found to be nesting in the study area. Several large avian raptors do nest in the study area, however, including the Golden Eagle, Red-tailed Hawk, Ferruginous Hawk, Swainson's Hawk, Cooper's

Hawk and Prairie Falcon. These birds often nest close to the Horned Owl nests. Examples of nesting proximity include a Red-tailed Hawk nest situated on a ledge 25 yards from a Horned Owl cave nest, a Ferruginous Hawk juniper nest approximately 100 yards below a Horned Owl cliff nest, and a Horned Owl sharing quarry nesting sites with Golden Eagles and Prairie Falcons.

Interaction was observed in only one instance, wherein a Red-tailed Hawk attacked a flushed Horned Owl. There was no apparent injury to either bird, although both nests were later abandoned by the 2 nesting pairs.

PREDATION

Hunting activity of Horned Owls was often observed normally in late evening after sunset. Although there was some hunting in the hills and canyons, the principal prey procurement activity occurred in the deserts. Owls were observed to hunt either alone or in pairs, employing one of two hunting techniques. One method consisted of flying slowly, harrier fashion, over the ground, diving suddenly on prey spotted; the other method consisted of perching on suitable elevated objects such as telephone poles, rock outcroppings, and road banks to facilitate sighting of prey which would then be attacked by a direct flight to it.

Food items recorded were either prey remains found in the nest or items identified from pellets removed from the nest sites for analysis. A total of 173 food items was recorded; this included 101 prey remains and 72 items based on pellet analysis. Mammals recorded from pellets were counted only on the basis of skulls present, thus avoiding possible duplication of individuals. Table 8 lists the prey items found, along with percentage calculations based on numbers of individuals of each species relative to the total number of prey items, without regard to volumetric considerations.

Mammals comprised 156 items, or 90.2 percent of the total food intake. The Black-tailed jackrabbit (*Lepus californicus*) and desert cottontail (*Sylvilagus auduboni*) accounted for 67 items or 38.7 percent of the total of all items. This was equalled by the kangaroo rat (*Dipodomys ordii*), which totaled 68 items or 39.3 percent of the total food items. Other mammals less frequently recorded included the white-footed deer mouse (*Peromyscus maniculatus*), meadow mouse (*Microtus sp.*), ground squirrel (*Citellus towsendii*), and wood rat (*Neotoma sp.*).

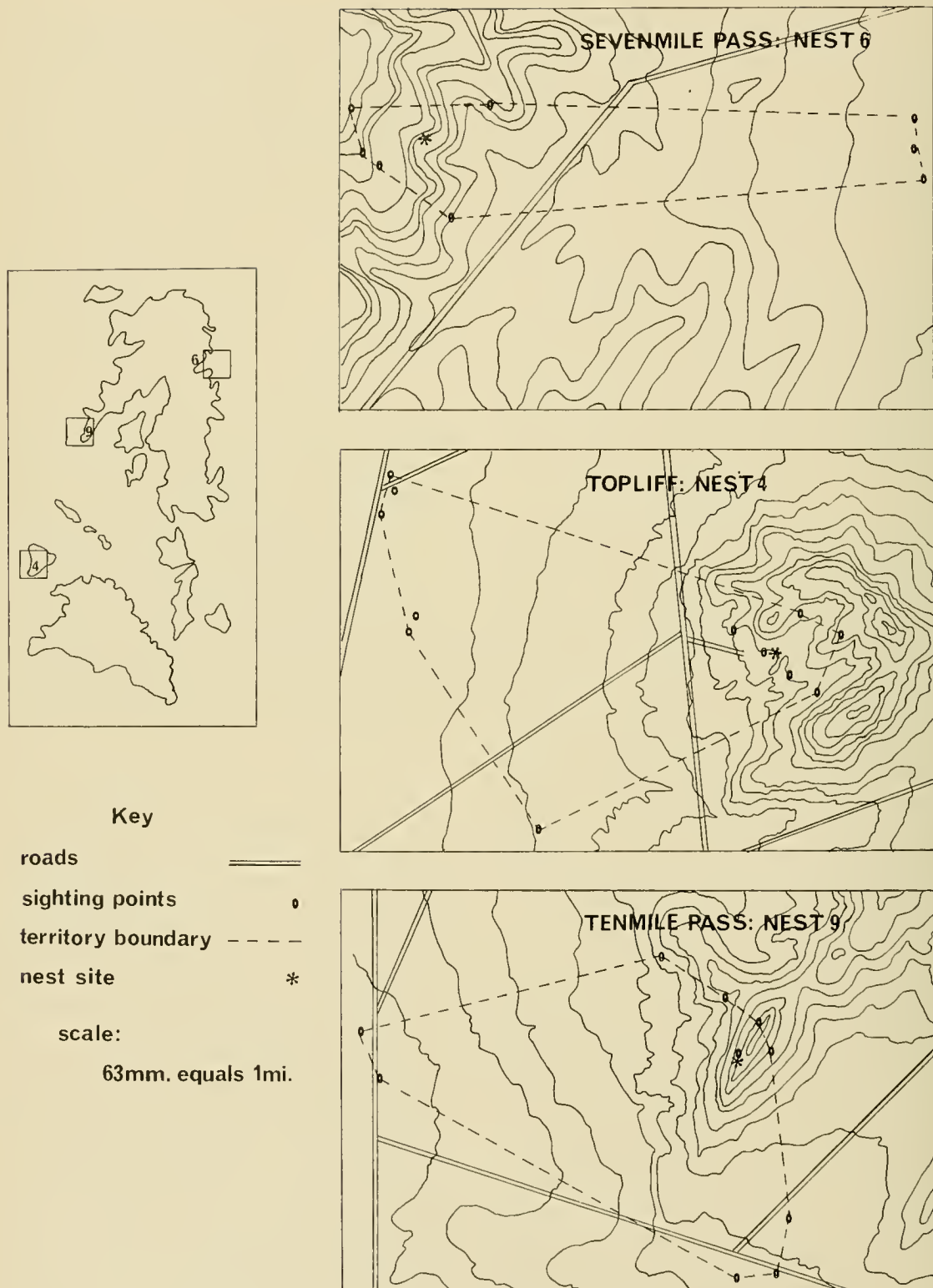


Fig. 7. Territories of three pairs of Great Horned Owls

TABLE 8
Food of horned owls in the study area

Prey species	Scientific name	Number of items	Percent of total items
Mammals			
Kangaroo Rat	<i>Dipodomys ordii</i>	68	39.3
Black-tailed Jackrabbit	<i>Lepus californicus</i>	41	23.7
Desert Cottontail	<i>Sylvilagus auduboni</i>	26	15.0
White-footed Mouse	<i>Peromyscus maniculatus</i>	13	7.5
Ground Squirrel	<i>Citellus townsendii</i>	4	2.3
Meadow Mouse	<i>Microtus sp.</i>	2	1.2
Wood Rat	<i>Neotoma sp.</i>	2	1.2
Total mammals		156	90.2
Birds			
Mourning Dove	<i>Zenaidura macroura</i>	3	1.7
Pinyon Jay	<i>Gymnorhinus cyanocephala</i>	2	1.2
Total birds		5	2.9
Invertebrates			
Scorpions	(unidentified)	12	6.9
Total invertebrates		12°	6.9

°present in 12 pellets

Only 2 species of birds were recorded, contributing 5 items or 2.9 percent of the total food items. Neither occurred in appreciable numbers, the Mourning Dove being represented by 3 specimens and the Pinyon Jay by only 2 specimens.

The only invertebrate representatives found belonged to a species of scorpion. Remains of these were found in 12 separate pellets, constituting 6.9 percent of the total prey items.

Volumetrically, the greatest single contributor of bulk food would be the black-tailed jackrabbit, followed by the desert cottontail. The kangaroo rat, although occurring in more numbers than both of the lagomorphs, would only constitute the third largest bulk contributor, owing to its smaller size, while the other mammals, birds, and invertebrates would contribute much less food.

DISCUSSION AND CONCLUSION

Nesting population densities for the 1967 and 1968 season were .36 pairs per square mile of study area and .40 pairs per square mile, respectively. Orians and Kuhlman (1956) found nesting densities of .22, .20, and .12 pairs per square mile in the cottonwoods of the Wisconsin plains. Errington, Hamerstrom, and Hamerstrom (1940) found .50 pairs per square mile in the same habitat type near Prairie du Sac, Wisconsin. Baumgartner (1939) estimated his study population in the cottonwood creek bottoms near Lawrence, Kansas, at 2.0 pairs per square mile. Fitch (1947) estimated a population in the California chaparral at 3.0 to 4.0 pairs per square mile. However, both of these latter investigations were based on the counting of

hooting birds, and neither was substantiated by an intensive search for nests.

The observations cited above indicate that the availability of nesting sites may play a key role in determining the possible Horned Owl nesting density. Smaller densities were found in areas of widely scattered potential nesting sites, while larger densities occurred in those areas offering the greatest number of possible sites. My findings seem to substantiate this, as I found the greatest concentrations of Horned Owl nests in the numerous cliffs lining the periphery of the hills, whereas the interior of the hills and the deserts provided fewer nesting sites, and thus supported fewer owls. However, nesting density may also be modified by food availability, a subject which was not investigated in this study.

Owls of the study area commonly used cliffs, quarries, caves and ledges for nesting sites. Similar site usage has previously been observed by Bent (1937), Bee and Hutchings (1942), and Dixon (1914), but utilization of abandoned quarries has not been previously reported, although Sugden (1928) did observe owls nesting in abandoned Indian cliff dwellings in southern Utah.

Baumgartner (1938), and Orians and Kuhlman (1956) feel that hawks play an important role in Horned Owl productivity by providing nests for their breeding. Although owls on the study area commonly used old Raven, Red-tailed Hawk, and Ferruginous Hawk nests, I feel that their use of cliff sites precludes the necessity of hawks building nests for them, as four of the study nests were on unimproved rock and most of the remainder of the nests being used were in such poor condition that they pro-

vided no actual benefits to the owl occupants. This conclusion is reinforced by my observations that these desert Horned Owls may use the same nest for several years in succession, whereas Orians and Kuhlman (1956) found that the owls of their study were unable to use old nests for more than one season, as the nests would become too dilapidated unless repaired by hawks.

BREEDING

Bent (1937) notes the average horned owl clutch size to be from two to three eggs, with one or four occurring uncommonly. In their later study, Orians and Kuhlman (1956) found a clutch size of two eggs to be the most common, with one-egg clutches appearing less frequently, and three-egg clutches rarely occurring. Bee (unpublished data) records Utah clutch sizes ranging from one to four eggs, with two appearing most commonly.

Bent (1937) further noted that egg-laying dates were between January and May, depending on the locality. My observations seem to indicate that both clutch size and egg-deposition date vary with yearly differences in winter temperature and severity, as there was a significant difference in egg-deposition dates (eggs were laid one full month earlier in the second-study year) and clutch size (from an average of 2 eggs to an average of 3 eggs per clutch) in the two years of study. However, further observations would be necessary to substantiate this hypothesis.

TERRITORY

My discovery of a male occupying his territory in December agrees with the findings of a number of observers, including Ridgway, Baird, and Brewster (1874), Errington (1932), Baumgartner (1938), and Orians and Kuhlman (1956), all of whom observed male Horned Owls occupying their territories in the late fall and winter.

The actual territory of these desert-dwelling owls seems to be larger than those found in previous studies. Ridgway, *et al.* (1874) noted that horned owls rarely go more than a mile from their nest sites. Miller's (1930) observations indicated that horned owls patrol an irregularly shaped territory with the largest diameter of no more than one half mile. Baumgartner (1938) obtained similar results, noting that his study birds also held territories of not more than a quarter mile radius in any direction from the nest site. I found that while the desert horned owls generally do not exceed a half mile

radius into or along the periphery of the hill sites, they do range widely into the deserts, with activity radii often exceeding one mile.

Both Baumgartner (1938) and Bent (1937) state that horned owls will not tolerate other avian predators nesting in proximity, but I found several instances of other raptors nesting within a hundred yards of horned owl nests. This included one example of a Red-tailed Hawk nesting only 25 yards from an active horned owl nest. However, in agreement with Baumgartner (1938) I found no other species of large owls nesting in the proximity of the horned owl nests, although both the Long-eared Owl and Short-eared Owl occur in the adjacent valleys.

PREDATION

The results of my predation studies agree with those of Errington, Hamerstrom and Hamerstrom (1940), Alcorn (1942), Fitch (1947), and Orians and Kuhlman (1956), who found that lagomorphs constitute the principle volumetric items in the horned owl diet. Bond's (1940) Nevada desert study demonstrated a similar utilization of several small species, including kangaroo rats, white-footed deer mice, meadow mice, and wood rats, but failed to show comparable use of rabbits and cottontails. I found that owls on the study area utilized fewer different species, but relied heavily on three species: the black-tailed jackrabbit, the desert cottontail, and the kangaroo rat.

SUMMARY

This study describes the nesting ecology of the Great Horned Owl, *Bubo virginianus* in the desert regions of western central Utah. Study aspects included population and distribution as determined by the location of all active nests in a unit area; territoriality as determined by observations from constructed blinds and sighting information; and predation as demonstrated by a tabulation of prey remains found in nests and analysis of pellets removed from the nest site. Data were gathered for a period of two nesting seasons, the spring of 1967 and the spring of 1968, in the Thorpe and Topliff Hills of Utah and Tooele Counties, Utah.

Owl nesting densities were found to be .36 nests per square mile in 1967 and .40 nests per square mile in 1968. Nest sites included cliff lines, abandoned quarries, and junipers. Cliff nests occurred most often, with the eggs deposited either on bare rock or in old Raven, Red-tailed Hawk, or Ferruginous Hawk nests.

Both egg-deposition dates and clutch size differed between the two years of the study period, with an average clutch of 2 eggs being laid in late March or early April in the 1967 season, and an increased average clutch of 3 eggs being laid in late January or early February in the 1968 season. In 1967 four nests produced eight young, all of which were successfully fledged. In 1968 ten nests produced 21 young, of which 15 fledged. Nesting failures were frequent in the second-study season, occurring in five of the ten study-area nests. Reasons for failure were attributed to human interference and avian interspecific competition.

The nesting pairs maintained large territories, often ranging over one mile from the nest site into the surrounding valleys. These owls apparently tolerate the close nesting of diurnal avian predators, but not other owls.

The black-tailed jackrabbit and desert cottontail contribute the bulk of the horned owl food, followed by the kangaroo rat. Other mammals, birds, and invertebrates are utilized to a lesser extent.

Economically these owls are of little importance to agriculture or game management in this area, but may contribute to range management through their predation on the lagomorph and rodent populations.

NESTING ECOLOGY OF THE FERRUGINOUS HAWK *BUTEO REGALIS*

by

John Bradford Weston

INTRODUCTION

The Ferruginous Hawk (*Buteo regalis*) is the largest and most powerful of the North American buteos. It is a bird of the western plains and arid regions, breeding from southwestern Canada to southern Arizona, New Mexico, and Kansas. It winters from California and Montana to Lower California and northern Mexico, seldom occurring east of the Mississippi River.

The Ferruginous Hawk may live on grassy prairies where it nests in the timber belts along the streams, or in the barren, treeless plains or badlands where it usually builds its nest on some convenient cliff, butte, or cutbank. Its chief habitat requirement seems to be a good supply of small rodents on which it characteristically feeds (Bent, 1937).

Fuertes (1920), May (1935), Bent (1937), Sprunt (1955), and Grossman (1964) have each described some phases of the natural history of this species. Bowles (1931) described ground and tree nesting of the Ferruginous Hawk in Washington. Cameron (1914) described nest sites and food preferences of this species in Montana. Salt (1939) listed migration routes of hawks banded in Alberta, Canada. To date, however, I have found no work that

adequately covers the nesting ecology of the Ferruginous Hawk.

The purpose of this study is to furnish more information on the nesting ecology of the Ferruginous Hawk in Utah, with particular attention being paid to distribution, density, and nest sites. Observations on territorial behavior, feeding mechanics, nest behavior, hunting techniques, and mortality were also included.

THE STUDY AREA

The study area embraces some three townships and three ranges of desert and semidesert land immediately south and west of Fairfield, Utah County, west central Utah (Fig. 8). The major portion of the area is formed by Cedar Valley and several ranges of low hills immediately adjacent to the valley. Topography is generally flat, broken only by the low hills. Elevation of the desert floor is about 4,900 feet above sea level. Within the eastern edge of the study area lie the Lake Mountains, and along the area's western edge the Topliff and Thorpe Hills are prominent. These mountains vary in altitude from 5,900 feet to 7,690 feet above sea level. To the north the Oquirrh Mountains rise well above 10,500 feet. The southern boundary

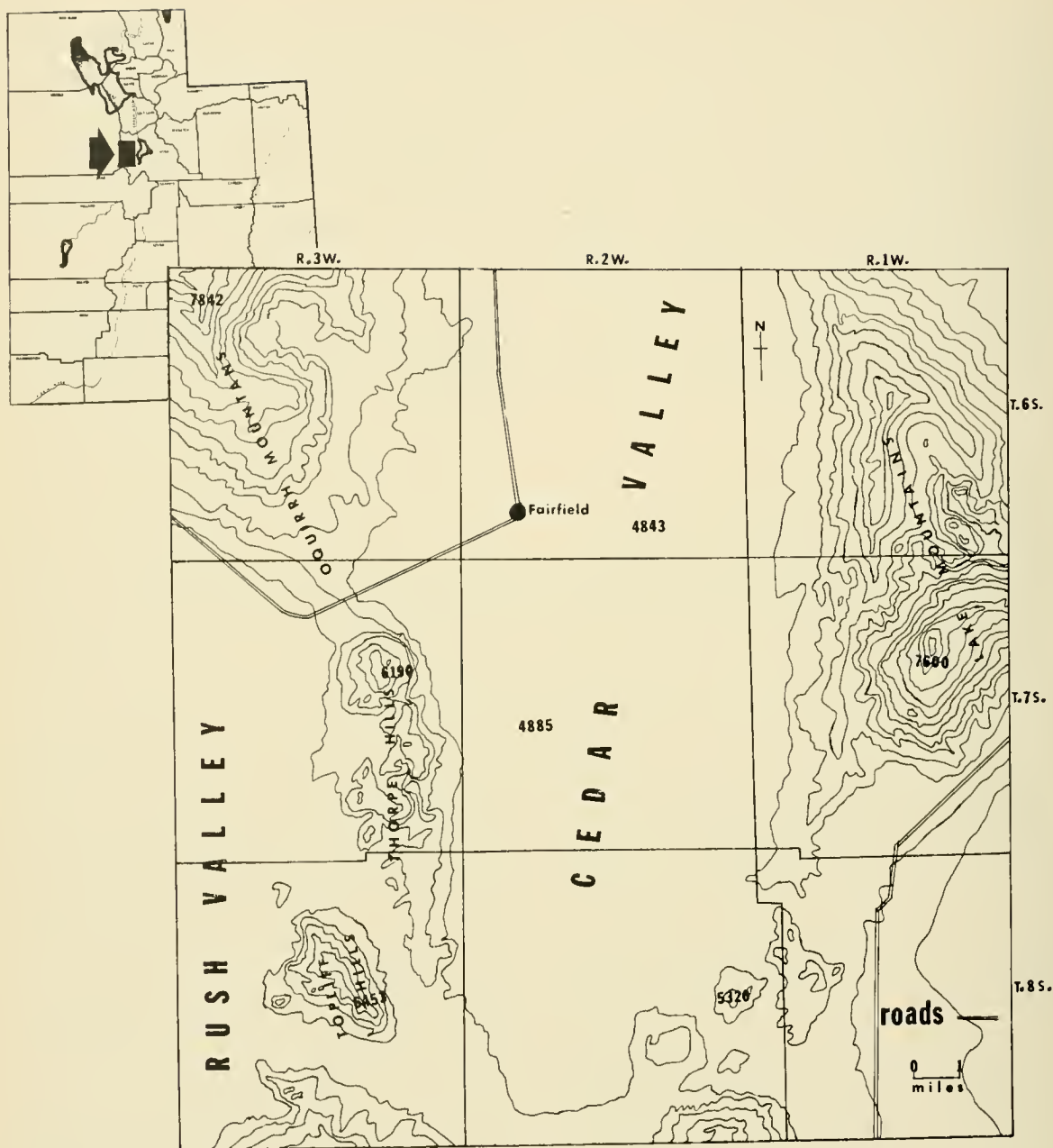


Fig. 8. Study area location

of the study area is an arbitrary line drawn through the southern portion of Cedar Valley and the adjoining hills. Agriculturally developed areas form portions of the northern and eastern boundaries.

METHODS AND PROCEDURES

Field work was conducted during the spring seasons of 1967 and 1968. During the spring of 1967, I spent nearly every weekend from February 20 through June 30 in the study area col-

lecting data. In the spring of 1968, field work was again conducted from late February through June 30. In the course of this two-year project, no fewer than 450 man-hours were devoted to the field studies.

Owing to the large size of the study area, a small portion was chosen in which a more detailed, intensive study could be conducted (Fig. 9). The area chosen for intensive study represents a typical portion of the larger, more general study area. It was chosen because it was

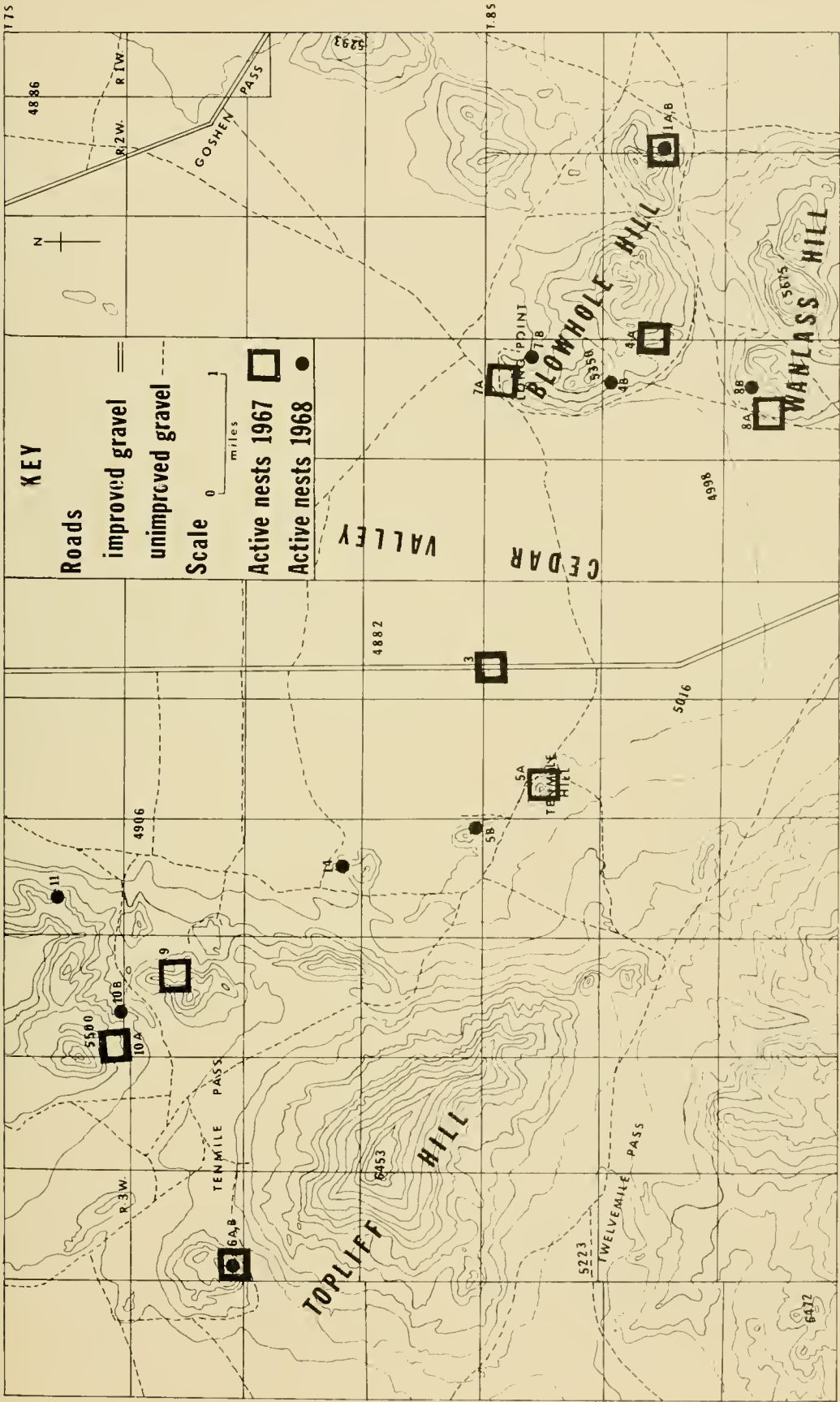


Fig. 9. Intensive study area nest site locations

easily accessible and contained a high density of nesting Ferruginous Hawks.

During the spring of 1967, a systematic search was conducted throughout the study area for Ferruginous Hawk nests. Behavior associated with hunting, courtship, and territorial defense of the hawks was often utilized in locating nests and delineating hunting ranges. Aerial surveys were also utilized to locate possible nest sites. Such surveys were valuable only to the extent of locating suitable nesting terrain.

After Ferruginous Hawk nests were located, those thought to be "active" or in use that year were kept under observation throughout the study. The remains of prey were observed and pellets were gathered from all nests in which they occurred. Pellets were also collected from roosting sites of the male hawks. Such sites were usually located near the nest.

Permanent blinds composed of a wire mesh frame with a burlap covering were placed upon hillsides above several nests. From these blinds observations were recorded on a portable tape recorder, and nesting activities were photographed with a 35mm. single-lens reflex camera equipped with several telephoto lenses ranging up to 600mm. in length.

Known breeding pairs of hawks were assigned numbers, and each nest of that pair was assigned the corresponding number and an alphabetical designation. Therefore, nest 1a, 1b, . . . 1d all belonged to pair number 1.

Analysis of prey remains and pellets was made by the writer. Bones were identified by comparison with those of known specimens. Pellets were analyzed on the basis of bones contained therein and the presence of general types of hair found. Where possible, all prey items were identified to species.

RESULTS

POPULATION AND DISTRIBUTION

During 1967-1968 the general study area supported 21 known pairs of Ferruginous Hawks for an average density of one pair per 15.4 square miles. These figures express the maximum area per pair, for areas inhabited by humans are included, and unknown nesting pairs may also have been present. The majority of the hawks nested in the foothills surrounding Cedar Valley. The valley floor, which comprises a major portion of the study area, is essentially void of suitable nest sites.

The smaller intensive study area supported 11 known pairs of hawks for an average density of one pair per 7 square miles. Again, Cedar

Valley comprised a large portion of the study area, with the hawks nesting in the foothills on its perimeter.

Seasonal displacement

The Ferruginous Hawk population in the study area was present at a high density only during the nesting season, which lasted from early March to late July. By September 1 no Ferruginous Hawks were observed in the study area. Several intensive searches conducted during the winter of 1967-68 revealed the presence of only one Ferruginous Hawk in the west desert area of central Utah. This bird was located some 25 miles west of the study area.

By mid-November a large population of raptors presumed to nest in more northerly areas had moved into the study area and surrounding terrain. The Rough-legged Hawk (*Buteo lagopus*) and the Bald Eagle (*Haliaeetus leucocephalus*) were present in particularly large numbers. These raptors remained in the area until late February and early March, when they departed and were replaced in part by Ferruginous Hawks which had presumably wintered farther south. Also occupying the study area only during the spring and summer months were the Red-tailed Hawk (*Buteo jamaicensis*), Swainson's Hawk (*Buteo swainsoni*), and Sparrow Hawks (*Falco sparverius*). The Golden Eagle (*Aquila chrysaetos*) and Great Horned Owl (*Bubo virginianus*) were permanent residents of the area throughout the study.

Fish and Wildlife Service locktite bands were placed on nesting hawks during the 1968 season. No recoveries which might indicate direction of seasonal movements had been made by the end of this study.

NEST LOCATIONS

Nest distribution

Ferruginous Hawk nests, often very old and in poor condition, were located on most low hills and many in scattered trees throughout the study area. However, occupied nests occurred in groups. That is, one portion of a large habitat area contained a series of active nests, while another nearly identical portion of the same habitat contained only old inactive nests. Active nests occurred in the same areas during both years of study. The Tenmile Pass and Blowhole Hill-Long Point areas exhibited a high concentration of active nesting pairs during the present study.

Proximity of Nests

The maximum and minimum distances between nearest neighbors for 13 occupied nests

TABLE 9
Number (and percentage) of Ferruginous Hawk nests in various sites

Nest sites	1967				1968				All nests*			
	Unoccupied		Occupied		Unoccupied		Occupied		Unoccupied		Occupied	
Ground	18	(58)	8	(62)	24	(69)	6	(43)	42	(64)	14	(52)
Juniper	11	(35)	4	(31)	9	(26)	7	(50)	20	(30)	11	(40)
Cliff	1	(3)	1	(7)	2	(5)	0	(0)	3	(5)	1	(4)
Cliffrose	1	(3)	0	(0)	0	(0)	1	(7)	1	(1)	1	(4)
Totals	31	(100)	13	(100)	35	(100)	14	(100)	66	(100)	27	(100)

*This information was recorded for all nests, regardless of the years of construction, occupation, or abandonment.

in 1967 were 2.3 miles and 1.1 miles, respectively. In 1968 the maximum distance was 2.4 miles, and the minimum distance of 0.4 mile separated two nests on the same long hill, one facing south and the other north (Fig. 9, Nests 4b and 7b).

Supernumerary (alternate) nests were found for 25 nesting pairs, or 93 percent of 27 occupied nests visited during 1967 and 1968. The hawks often constructed entirely new nests each year. In 1967, 58 percent of the occupied nests had been entirely constructed during the spring of that year. In 1968 43 percent of the occupied nests were new, even though older nests were repaired and attended regularly until eggs were laid. Pairs with more than one nest had an average of 2.6 supernumerary nests. One pair attended five nests, no two of them farther apart than 0.1 mile; 4 pairs had one supernumerary nest each; the remaining 22 pairs had two or three additional nests.

NEST SITES, COMPOSITION, AND SIZE

Of the 27 occupied nests found, 52 percent were located on the ground (Table 9). As a general rule, these nests were easily accessible from nearly every direction. The next most common nest site (11 active nests) was the Utah juniper, a tree characterized by large limbs that provide ideal support for the heavy, bulky nests. Juniper nests were usually located from six to ten feet above the ground. Unoccupied nests were classified as Ferruginous Hawk nests if they were constructed in the habitat preferred by this species or if they contained Ferruginous Hawk feathers.

In 1967 6 of 11 active nests were on eastern exposures, 2 faced west, 2 faced south; and although several hills with northern exposures were available, only one nest was found on them (Table 10). Differences observed in 1968 were negligible.

The typical nest is usually composed of sticks varying in size from that of a twig to those an inch or more in diameter (Fig. 10).

TABLE 10
Exposures of occupied nests, 1967-1968

Year	Direction of exposure*							
	N	North (Percent)	N	East (Percent)	N	West (Percent)	N	South (Percent)
1967	1	(9)	6	(55)	2	(18)	2	(18)
1968	1	(9)	6	(55)	1	(9)	3	(27)

*Applies only to tree and ground nests located on hill-sides.

The lining is generally of juniper bark or bunch grass. One nest was lined with sheep's wool. Sixty-five percent of the active nests observed during the study had incorporated at least one piece of paper into the nest pocket. Most nests also contained pieces of dried manure. Juniper, shadscale, and big sagebrush, the most common plants in the area, provide most of the materials used in nest building.

After nesting activities had terminated in early summer, the dimensions of 24 active nests were measured and recorded. No trend in size variation could be distinguished between ground and tree nests. The average nest had a diameter of 39 inches, a thickness of 17 inches, a pocket diameter of 14 inches, and a pocket depth of 3 inches. The largest nest measured, a tree nest, had a diameter of 48 inches, a thickness of 43



Fig. 10. Nest 4b, a typical Ferruginous Hawk nest with a paper lining, April 1, 1968.

inches, a pocket diameter of 17 inches, and a pocket depth of 4 inches. The smallest nest measured, a ground nest, had a diameter of 29 inches, a thickness of 8 inches, a pocket diameter of 11 inches, and a pocket depth of 2 inches.

INITIAL NESTING ACTIVITY

The earliest date in 1967 that hawks were observed near their nest sites was March 6. The first nesting pair observed in 1968 was seen February 25. In both 1967 and 1968 March was the month in which nearly all nests were constructed, with most of them being essentially completed by March 25.

Three different pairs of hawks were observed building their nests. In each instance both members of each pair were active in nest construction. Sticks of various sizes, which made up the bulk of every nest, were always carried to the nest site in the hawks' feet. On one occasion a strip of bark was seen to be carried to the nest in a hawk's bill. The female, distinguished by her larger size, did the actual arranging of materials in the nest. Once nest building had begun, each pair spent several hours every day carrying material to the nest until it was finished.

PRODUCTIVITY

Clutch size

In 1967 thirteen nests produced 20 eggs for an average of 1.5 eggs per nest. One nest produced 4 eggs, two nests produced 3 eggs, five nests produced 2 eggs, and the remaining five nests were abandoned before any eggs were laid.

In 1968 fourteen nests produced 50 eggs, an average of 3.57 eggs per nest. Eleven nests contained 4 eggs, two nests contained three eggs, and the remaining nest was abandoned before any eggs were laid (Table 11).

Hatching, fledging success, and description of young

In 1967 a total of thirteen nesting efforts produced 8 young, an average of .67 young per nest. Of those hatched 8 (100 percent) fledged.

In 1968 fourteen nesting efforts hatched 33 young for an average of 2.36 per nest. Of those hatched 28 (85 percent) fledged, an average of 2 fledged per nest (Table 11).

Within hours after hatching, the young hawks exhibited a dense covering of white down. Their gapes were noticeably broader than those of other species of hawks of similar size. Their cerea were greenish-yellow and their irises were dark gray. Pin feathers began to appear between

the eighth and twelfth days and full juvenile plumage had developed by the seventh week.

Observed dates of reproductive activity

During both 1967 and 1968 every pair of hawks had selected its nest site by March 10. In 1968 the average laying date was April 8, the average hatching date was May 10, the average brood departure date was June 25, and the resulting average number of days in the nest was 45. Those differences observed in 1967 were probably not significant (Table 12).

BEHAVIOR

Territorial behavior

The observations on territorial behavior seemed to be rather inconclusive. At times each pair was seen to vigorously defend its territory against any intruding raptor. On other occasions predatory birds flew directly over active nests without eliciting any response whatsoever from the occupant pair. On one occasion two Swainson's Hawks were seen to attack a soaring male Ferruginous Hawk whose mate was sitting with her three young on a nest directly below him. The intruding Swainson's Hawk flew high

TABLE 11
Eggs laid, young hatched, and young fledged,
1967-1968

	Years	
	1967	1968
Number of nesting efforts	13.00	14.00
Number of eggs laid	20.00	50.00
Average number of eggs per nest	1.50	3.57
Number hatched	8.00	33.00
Average number hatched per nest	0.67	2.36
Number fledged	8.00	28.00
Average number fledged per nest	0.67	2.00
Percent of hatched that fledged	100.00	85.00

TABLE 12
Observed dates of reproductive activity of the
Ferruginous Hawk on the Utah study area.

	Years	
	1967	1968
First selection of nesting territory	III/6	II/25
Earliest laying date	IV/3	IV/4
Latest laying date	IV/15	IV/19
Average laying date	IV/10	IV/8
Earliest hatching date	V/9	V/6
Latest hatching date	V/17	V/22
Average hatching date	V/12	V/10
Earliest brood departure date	VI/18	VI/12
Latest brood departure date	VI/27	VII/5
Average brood departure date	VI/23	VI/25
Average number of days in nest	43	45
Breeding season, span (days)	115	132

above the resident Ferruginous Hawk, then swooped on him at steep angles, barely missing him several times. Finally, one of the Swainson's Hawks came too close and was grasped in the talons of the larger Ferruginous Hawk, who immediately released him. Upon being released, the Swainson's Hawk tumbled several feet, regained his balance and quickly flew away, followed closely by his partner. The Ferruginous Hawk returned to his leisurely soaring flight above the nest.

On five occasions as I visited five separate active nests, three adult Ferruginous Hawks soared above me, screaming, diving, and protesting my presence. At no time was hostility exhibited by the nesting pair toward the third hawk that had joined them in their attack on me. These were the only instances in which more than two Ferruginous Hawks were observed above any one nest site.

Several times during the study Ravens (*Corvus corax*) were attacked by nesting hawks, although no actual contact was ever observed. On one occasion a Golden Eagle was chased from a Ferruginous Hawk's nest site, although eagles were generally tolerated wherever they roamed.

Nest behavior

Only female hawks were observed incubating eggs, although the males may have participated in incubation during periods of my absence. Both members of each pair hunted prey for their young, but the male always left his catch on the edge of the nest and departed. By contrast, when the female carried prey to the nest, she remained to feed the young.

Throughout incubation and while the young were covered with down, the female remained at the nest almost constantly. However, as the young grew older and more self-sufficient both parents spent increasing amounts of time soaring and roosting together in areas near the nest. As the young reached their sixth week after hatching, the female was present at the nest only during the night time and on subsequent short visits to bring food to the nest during the day.

FOOD HABITS

Remains of prey were counted, recorded, removed from the nest, and identified. When possible, food was squeezed from the crop of nestlings (Errington, 1932). Pellets regurgitated by both adults and young were counted, collected, and stored. However, pellet analysis is a poor method of determining quantitatively the food of nestling hawks, for such pellets contain very

little osseous material. Prey species can be identified readily from most pellets, but it is frequently impossible to determine the number of individuals concerned. In all, 219 samples were taken from 26 eyries, which included 53 pellets and numerous parts and pieces of rabbits and other prey. From these, 283 prey specimens, or 1.3 per sampling, were identified, indicating the minimum number of individuals that the various identified items could represent.

Identified prey

Of the 283 prey specimens identified, 92 percent were mammals (Table 13). Kangaroo rats comprised 48 percent of the mammals and 44 percent of all prey items. Black-tail jackrabbits were the next most plentiful, representing 33 percent of the mammals and 30 percent of the total. It is likely, however, that jackrabbits represent the greatest amount of food material in the diet of these hawks. Birds composed 5 percent of the total number of prey items, with Horned Larks the most prevalent, representing 86 percent of the birds. The only reptiles tallied were 3 snakes and 6 horned lizards, representing only 3 percent of the total number of prey individuals.

Hunting techniques

The most common hunting technique exhibited by this species was to fly low over open country, never rising more than a few feet above the ground, with rapid wingbeats propelling it swiftly forward. Capture was attempted of any small animal encountered in the flight path.

I often saw Ferruginous Hawks soaring in true *Buteo* style. On one occasion a soaring hawk swooped on a black-tail jackrabbit, which it missed. Twice during my study, hunting hawks were observed to hover in one place by rapid vibration of their wings, then fly on a few feet and repeat the procedure until prey was found and captured.

Observation of several nests from concealed blinds revealed that intensive hunting was usually initiated at first light of dawn, often being completed by sunrise. Evening hunting usually started at sundown. Food demands by nestling hawks necessitated extended hunts as the nesting season progressed.

MORTALITY

During this study several dead raptors were found. A fellow student conducted a mortality census of raptors along a utility pole line located in the center of my study area (Ellis, *et. al.*, 1969). In 1967-1968 he counted 28 dead raptors (primarily eagles) along the nine-mile stretch

TABLE 13
Food of nesting Ferruginous Hawks in the west-central Utah study area^o

Prey species	1967		1968		Total	
	No.	Percent	No.	Percent	No.	Percent
Mammals						
Ord Kangaroo Rat (<i>Dipodomys ordii</i>)	31	40	93	45	124	44
Black-tail Jackrabbit (<i>Lepus californicus</i>)	23	30	62	30	85	30
Antelope Squirrel (<i>Citellus leucurus</i>)	5	6.5	10	4.8	15	5.3
Deer Mouse (<i>Peromyscus maniculatus</i>)	4	5.2	11	5.3	15	5.3
Desert Cottontail (<i>Sylvilagus audubonii</i>)	2	2.6	5	2.4	7	2.4
Pocket Mouse (<i>Perognathus parvus</i>)	1	1.3	6	2.9	7	2.4
Rock Squirrel (<i>Citellus variegatus</i>)	2	2.6	3	1.4	5	1.7
Harvest Mouse (<i>Reithrodontomys megalotis</i>)	0	0.0	1	.4	1	.1
Long-tail Weasel (<i>Mustela frenata</i>)	0	0.0	1	.4	1	.1
TOTALS	68	88.2	192	92.6	260	92.3
Birds						
Horned Lark (<i>Eremophila alpestris</i>)	3	3.9	9	4.3	12	4.2
Green-tailed Towhee (<i>Oberholseria chlorura</i>)	0	0.0	1	.4	1	.1
Say's Phoebe (<i>Sayornis saya</i>)	0	0.0	1	.4	1	.1
TOTALS	3	3.9	11	5.1	14	4.4
Reptiles						
Horned Lizard (<i>Phrynosoma platyrhinos</i>)	6	7.8	0	0	6	2.1
Gopher Snake (<i>Pituophis melanoleucus</i>)	0	0.0	2	.9	2	.2
Western Whipsnake (<i>Masticophis lateralis</i>)	0	0.0	1	.4	1	.1
TOTALS	6	7.8	3	1.3	9	2.4

^oBased on 219 samplings taken from 26 nests.

of poles, which was paralleled by a gravel road. The only Ferruginous Hawk mortality recorded during this project was an adult female shot at nest #3. As indicated by data previously cited in Table 11, nestling mortality did not appear to be excessive.

DISCUSSION AND CONCLUSIONS

The present study revealed a sizable population of Ferruginous Hawks in the west desert study area during the years of 1967 and 1968. Twenty-one pairs of hawks, or one pair per 15.4 square miles, were located. It should be noted that Cedar Valley, which embraces a large part of the study area and is essentially devoid of nests, was included when area-per-pair calculations were computed; this leads to indications of a larger area per nest pair than was actually utilized. Although present literature gives no indication of population densities in other areas, I assume that this population is representative of areas exhibiting similar habitat conditions.

An annual seasonal displacement was exhibited. Raptors from more northerly nesting grounds migrated into the study area during the winter months. They replaced the nesting population of Ferruginous Hawks, which had essentially departed from the nesting area by early September. Spring migrations brought the Ferruginous Hawks back to their nesting grounds by early March.

Salt (1939) banded 114 juvenile Ferruginous Hawks in Alberta, Canada. Band returns indicated that the wintering range of these birds included New Mexico, Colorado, Kansas, Texas, and Oklahoma. A single bird was recovered in the southwest corner of California. One bird, almost three years of age, was subsequently recovered within a dozen miles of its birthplace. He was unable to secure the body of the bird for dissection and examination which might have proved whether or not it was a breeding bird.

By the end of this study, no bands had been recovered from juvenile hawks banded in the west-central Utah study area. However, I assume that the hawks of this area pursued a southerly migration route similar to that of their Canadian counterparts.

Deserted nests indicate that Ferruginous Hawks have at some time, past or present, nested in essentially all suitable areas surrounding Cedar Valley. Current active nest locations, however, imply a preference to inhabit particular areas instead of dispersing in a random distribution pattern. Food availability and potential nest site locations seem to be uniformly distributed throughout the area, thus discounting these as major determining factors in site locality preferences.

The characteristic nest location of this species in the study area is upon the ground on the sides

or summits of low hills. If constructed on the summit of a hill, it is usually situated atop a rock, and if on the side of a hill, a jutting ledge of rocks forming a natural shelf is selected to hold the bulky, loosely-constructed nest in place (Fig. 11). Behle, Woodbury, and Cottam (1943) describe ground nests located along the 1846 route of the Donner Party on the Great Salt Lake Desert north of Knolls, Utah. These nests varied in size up to 6 feet in height and 9 feet in diameter at the base and were composed of *Allenrolfea* roots and stems. The second most common type, the juniper nest, closely resembles the ground nest. It is usually constructed five to eight feet above the ground (Fig. 12). Nests similar to those found in the present study area are described by Cameron (1914) in Montana and Bowles (1931) in Washington. Bent (1937) describes nests in North Dakota which were situated 40 feet above the ground in tall swamp oaks. Nests I observed were composed of heavy sticks, manure, and other rubbish, and lined with grass, strips of bark, and paper. Williams and Matteson (1947b) recorded a nest lined with paper in Wyoming. They also reported that nests located by Wyoming biologists in the year 1880 were composed almost entirely of dried buffalo bones.

During the present study, 17 of 22 active nests were on southern or eastern exposures. These data suggest that nest site preference is influenced by the direction of the sun's rays. Exposure should be important during the early spring months. Even in the warmer months of June and July, nests facing south and east might be preferable. Those with easterly exposures would receive the warm morning sun and be shaded in the hot afternoons. McGahan (1968) found that most of the Golden Eagle nests in his study area faced either south or east.



Fig. 11. Nest 5b, a Ferruginous Hawk ground nest in the west-central Utah study area, June 24, 1968.



Fig. 12. A Ferruginous Hawk Juniper tree nest in the west-central Utah study area, May 30, 1969.

Direction of nest exposure seems to be a major factor in determining proximity of nests of neighboring pairs. Nests exposed to the same hunting areas were constructed no closer than 1.3 miles, whereas nests facing different hunting areas were constructed as close as 0.4 mile apart.

Weather, prey densities, and human interference may each be partially responsible for the dramatic variation in productivity experienced between 1967 and 1968. It may well be that inclement weather factors such as low temperature, high humidity, or a violent storm may occur at a critical period in the hawk's reproductive cycle, thereby affecting its reproductive capability. Bee (1935) noted that at times hawks of this species would abandon their nests during inclement weather. Weather data obtained from the Brigham Young University Physics Department revealed little variation in monthly temperature and precipitation averages during this study. However, day-to-day variations obviously occurred and may have had marked influence on hawk productivity.

Another influencing factor may have been variable densities in prey populations present

during each of the two years, but no data on prey densities was gathered during this study.

Human interference may also have been a factor in productivity variations. In 1967 three nests containing eggs and four nests ready for eggs were abandoned early in the nesting season after one visit to each nest by the author. Although identical nest observation procedures were conducted again in 1968, no nests were abandoned. This leads me to believe that the human interference factor was negligible both years.

Ferruginous Hawk pair #3 nested in the center of Cedar Valley atop the two foot high road-bank of a well-traveled, improved gravel road. Two days after the initial discovery of the nest the female was found shot and killed at the nest site. Both of her legs and five rectrices had been removed (Weston and Ellis, 1968). This is the only known instance of direct human interference with nesting hawks during the study.

Both members of each pair participated in most nesting activities, exceptions being that only female hawks were observed incubating eggs and feeding the young.

Reproductive activity began with territory selection in early March and ended when the young were fledged in late June. The average incubation period was 32 days, which is 5 days longer than the 27-day average recorded by Cameron (1914).

In 1968 nest #13, which contained a single fifteen-day-old hawk, became too bulky for the juniper in which it was located and fell from the tree. The adult hawks quickly remedied the situation by constructing a crude ground nest directly under the original tree. The young hawk remained in this nest until it successfully fledged on June 24. Also of special interest in 1968 was nest #11, constructed in a juniper by a melanistic male and a light-colored female. Four young were fledged from the nest, three exhibiting

total melanistic plumage and one possessing characteristic light-colored plumage (see Frontispiece). This is especially intriguing in view of the fact that this was the only nesting melanistic adult in my study area and that the pair produced the only melanistic young observed during the study. Bent (1937) found that 50 percent of the hawks of this species observed in North Dakota were melanistic.

Territorial behavior appears to depend upon the mood of the hawks. Various raptors were often allowed to fly over the nest site throughout the nesting season, and during my visits other Ferruginous Hawks were allowed to come into the nesting territory to join the resident pair in attacking me. On other occasions, however, any bird that ventured near the nesting area was immediately attacked.

Ferruginous Hawk food-habit data indicate that mammals make up the bulk of the hawks' diet, with kangaroo rats and black-tailed jackrabbits comprising 74 percent of the total prey consumed. These findings seem to agree with other researchers, for May (1935) found this species to eat primarily mammals, but observed that in one area it was a conspicuous enemy of the California Clapper Rail (*Rallus longirostris*). Bent (1937) indicates that its food consists almost exclusively of mammals, ranging in size from jackrabbits to meadow mice. Cameron (1914) reported that in eastern Montana this hawk feeds chiefly upon prairie dogs and meadow mice. He saw Ferruginous Hawks kill a jackrabbit which they could not carry away. However, during the present study several adult jackrabbits were observed in different nests.

Hunting is usually conducted in this area before sunrise and after sunset of each day, indicating that the Ferruginous Hawk is primarily crepuscular in its hunting activities. This explains why a nocturnal animal such as the kangaroo rat is so often captured as prey.

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**Brigham Young University
Science Bulletin**

**OSTEOLOGICAL AND MYOLOGICAL COMPARISONS
OF THE HEAD AND THORAX REGIONS OF
CNEMIDOPHORUS TIGRIS SEPTENTRIONALIS BURGER
AND *AMEIVA UNDULATA PARVA* BARBOUR AND NOBLE
(FAMILY TEIIDAE) ^c**

by

Don Lowell Fisher ^o

and

Wilmer W. Tanner ^v



BIOLOGICAL SERIES — VOLUME XI, NUMBER 1

JUNE 1970

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INTRODUCTION

There has long been a need for a comparative study of the osteological and myological structures of the reptilian family Teiidae. This present study is organized to increase our understanding of the anatomical features of the head and thorax regions of two large genera of this large and diversified family. The two genera discussed are *Cnemidophorus* and *Ameiva*.

Although the entire family is in need of a comparative study, these two genera were chosen because they are, according to Burt (1931b), closely allied and also because a number of study specimens were available. The study is limited to the head and thorax regions inasmuch as this area, according to Patten (1951), seems to be the most plastic region of the body as far as adaptive radiation is concerned. We are aware that other regions of the vertebrate body are also plastic in some groups; however, we believe that in this family the thorax region is of special significance to the study of the phylogenetic development of genera within this family.

Studies dealing with taxonomy, physiology, ecology and general anatomy of the two genera have been made by various workers. Those reports which are pertinent to this study are cited below.

An extensive taxonomic study of the genus *Cnemidophorus* was made by Burt (1931b) with complete synonymy of the various species and subspecies to that date. A revision of the genus *Ameiva* was completed by Barbour and Noble (1915). Smith and Laufe (1946) in their summary of the Mexican lizards of the genus *Ameiva* dealt with the taxonomy of the genus. It will not be necessary, therefore, to give a detailed account in this report of the taxonomy which has been completed to date. We can thus confine ourselves more to the comparative anatomical aspects of the two genera.

The family Teiidae was established by Gray (1825), and today consists of about 40 genera (Smith and Taylor, 1950). The genus *Ameiva* was established by Meyer (1795) with *Lacerta americana* Seba = *Ameiva ameiva* (Linnaeus) being the genotype. According to Smith and Taylor (1950), there are 13 species and 28 subspecies in the genus.

The genus *Cnemidophorus* was established by Wagler (1830). The genotype is *Seps murinus* Laurenti. There are about 18 species of *Cnemidophorus* with about 47 subspecies (Smith and Taylor, 1950). Since 1950 only a few new species and subspecies have been described in each genus.

Ameiva undulata parva was established by Barbour and Noble (1915). The type is MCZ 5831 (with Van Patten as the collector) and the type locality is listed as Guatemala; however, this was later restricted by Smith and Laufe (1946) to Mazatenango. The range is

on the Pacific slopes from the Isthmus of Tehuantepec in Oaxaca south to Costa Rica.

Cnemidophorus tigris septentrionalis was established by Burger in 1950. The type is CNHM 38217 and the type locality is Una, Garfield County, Colorado. The range extends over the Colorado Plateau (Maslin, 1959b) and includes the northern half of Arizona, the northwestern quarter of New Mexico, the southeastern half of Utah, and the southwestern quarter of Colorado (Burger, 1950).

A synopsis of the genus *Cnemidophorus* was first completed by E.D. Cope (1892b) wherein he made a most memorable statement to all individuals who further attempt to resolve the phylogenetic relationships within this genus. He considered the discrimination of the species within *Cnemidophorus* the most difficult problem in herpetology.

A later work by Burt (1931b) using Ecology, scutellation, and distribution has helped in unravelling some of the problems of the phylogenetic relationships within the genus *Cnemidophorus*. Other large and comprehensive works on groups within the genus *Cnemidophorus* also have been recently completed. These include a report by Zweifel (1959) on the distribution and variation of the *sacki* group, a systematic study of the *deppei* group (Duellman and Wellman, 1960), and a systematic study of the *sexlineatus* group (Duellman and Zweifel, 1962). These works all analyze such characters as scutellation, coloration, dorsal patterns, size, and distribution.

The systematic relationships of the genus *Ameiva* have also been explored by Barbour and Noble (1915), who published an extensive work on the phylogeny and provided a description of the species and subspecies included in the genus. The relationships of the *Ameiva undulata* group were suggested by Stuart (1942). In this study he includes a diagnosis of each species as well as a key to the species.

A summary of the Mexican species of the genus *Ameiva* was published by Smith and Laufe (1946). Their report is informative, extensive, includes a historical summary and an analysis of characters by means of scutellation. A phylogeny, a key to the Mexican *Ameiva*, and an account of the subspecies is also included.

Some of the factors relating to behavior and evolution have also been reported. A thorough study for its time by Gadow (1906) on evolution was based on the Mexican species of *Cnemidophorus*. His report helps us to realize the great variety possible in a genus which has evolved in a land filled with the diversity of biotic conditions found in Mexico. Other studies include those by Broom (1925), Maslin (1959a, 1961, 1966), Zweifel (1962), Beargie and McCoy (1964),

Pennock (1965), Licht (1966), Lowe and Goldberg (1966), McCoy (1966), and Taylor and Medina (1966).

Much of the literature available on the family Teiidae deals with old and new collecting localities and taxonomy. Some such papers are those by Gray (1825), Boulenger (1884, 1899), Nopcsa (1928), Burt (1929, 1931a, 1931c), Beebe (1945), Smith and Burger (1949), Burger (1950), Smith and Taylor (1950), Maslin, Beidleman and Lowe (1958), Maslin (1963), Peters (1964), Zweifel (1965), and Stebbins (1966).

Fossil teiids have been reported by Brattstrom (1954), Etheridge (1960), Gehlbach (1965), and Romer (1966).

A number of anatomical works are of importance to those working in herpetology in the areas of osteology and myology. Among these are Boulenger (1891), Cope (1892a), Howes (1902), Bradley (1903), Broom (1903), Huntington (1903), Kingsley (1905), Kesteven (1919), Camp (1923), Reese (1923), Romer (1924), Sinsitsin (1928), Edgeworth (1931), Broom (1935), Davis (1936), Howell (1936), Gnanamuthu (1937), Dubois (1942, 1943), George (1948), Adams (1953), Poglayen-Neuwall (1954), Snyder (1954), Oelrich (1956), Romer (1956), Hofer (1960), Jollie (1960), Robison and Tanner (1962), Avery and Tanner (1964), and Romer (1964, 1966).

Although most of the anatomical works mentioned above do not consider extensively the family Teiidae, some are of special importance to a study of this family. Camp (1923) compares anatomically the families of reptiles and emphasized the genus *Tupinambis* as a member of the family Teiidae. Two other works of osteological import for the genus *Tupinambis* are those by Reese (1923) and Hofer (1960). To date, only one work has been published on the complete cranial osteology of *Cnemidophorus*, on *C. sexlineatus* and *C. gularis* by Dubois (1943). A major osteological report on *Ameiva* has not appeared to date. Taylor (1940) was one of the first to establish the presence of pterygoid teeth in *Cnemidophorus*. His study included nine species. Edmunds

(1960) presented the tooth replacement phenomena in lower vertebrates.

The myology of the family Teiidae has been studied only to a limited extent. Camp (1923) and Poglayen-Neuwall (1954) included work on *Tupinambis*, with a few references to the deep skull musculature of *Ameiva*. No comparative or descriptive study of the myology of *Cnemidophorus* or *Ameiva* has yet appeared. Perhaps the most extensive treatment of vertebrate cranial muscles is the work of Edgeworth (1935).

The position of the family Teiidae is unique in its phylogeny among the other saurians. This was observed by Stokely (1950) in his report on the occurrence of an intermedium in certain lizards. He found the intermedium present in several species of *Cnemidophorus*, but absent in *Ameiva ameiva praesignis*. Camp (1923) considered the presence of this wrist bone an indication of an older position in phylogeny. The apparent differences within the family Teiidae on this structure warrant a more detailed investigation. There is reason to believe that further osteological and myological studies of the family Teiidae should include comparisons with members of the family *Lacertidae*. The work of Uzzell (1959) and others suggest a parallelism that may be fruitful in phylogeny as well as anatomy.

The purpose of this paper, therefore, is to present a report on the anterior osteology and myology of a species of the genus *Ameiva* and to compare it with a species of the closely allied genus *Cnemidophorus*. It may thereby be possible to develop other criteria to be used in determining the phylogenetic relationships between *Cnemidophorus* and *Ameiva* within the family Teiidae.

We are grateful to Dr. Bertrand F. Harrison for his suggestions in preparing the manuscript and to Mr. Lee F. Braithwaite for his aid in the preparation of the illustrations. Dr. Robert T. Swenson and the X-ray technicians at the Utah Valley Hospital prepared the X-ray photographs of the wrist elements. We extend our thanks to the above and others who have aided us in this project.

MATERIALS AND METHODS

Cnemidophorus tigris septentrionalis Burger and *Ameiva undulata parva* Barbour and Noble are the principal species and subspecies used in this study. In the body of the text they will be designated as *C. t. septentrionalis* and *A. u. parva* respectively. Specimens of *Cnemidophorus tigris tigris* Baird and Girard and *Cnemidophorus tigris gracilis* Biard and Girard were also dissected for comparative purposes.

The specimens of *C. t. septentrionalis* were collected from southeastern Utah. Five came from North Wash near Hog Spring (BYU 31903-07); two from Star Spring (BYU 31908-09); one from Bullfrog Basin (BYU 31910); three from North Wash along highway U95 between Star Spring and Hanksville (BYU 31911-13) and nine from Snow's Canyon, west of Saint George, Utah (BYU 31914-22).

The specimens of *C. t. tigris* were collected in western Utah. Six specimens came from Lake Moun-

tain west of Utah Lake (BYU 31923-28), and one from Milford, Utah (BYU 31929).

The specimens of *C. t. gracilis* Baird and Girard examined were taken 11 miles east of Bowie, Cochise Co., Arizona (BYU 13555-61).

A. u. parva were collected at Finca Tinajas, Panzos, Alta Verapaz, Guatemala (BYU 14389, 14895-96, 14398, 14444, 14448-51, and 14453).

The specimens used for X-ray analysis of the wrist elements were the following: *C. t. septentrionalis* (BYU 31904); *C. t. gracilis* (BYU 13560); *C. t. canus* VanDenburgh and Slevin (BYU 30159); *C. t. aethiops* Cope (BYU 30196); *C. t. tigris* Baird and Girard (BYU 30552); *C. s. communus* Cope (BYU 24017); *C. s. gularis* Baird and Girard (BYU 12876); *C. d. deppei* Wiegmann (BYU 22541); *C. l. lineatissimus* Cope (BYU 24018); *C. l. lemniscatus* (Linnaeus) (BYU 22599); *C. exsanguis* Lowe (BYU 14158); *A. u. hartwegi* Smith (BYU 22523); *A. u. sinistra* Smith and Laufe (BYU 24013); *A. u. parva* (BYU 14398) and *A. aueri* Cocteau (BYU 30326).

Radiographs were taken with an X-ray machine using eleven milliamps at one and one-half seconds with a medium KVP. X-ray negatives were then enlarged in a slide projector and examined.

Skulls were cleaned by various methods. One specimen of *A. u. parva* (BYU 144451, snout-vent length 100 mm.) was skinned and placed in 35 percent ammonium hydroxide for two months, boiled for two hours and then cleaned by hand. It was then treated with Clorox bleach at full strength for 15 minutes with excellent results. Another specimen of *A. u. parva* (BYU 14450, snout-vent 86 mm.) as well as two *C. t. septentrionalis* (BYU 31924 and 31926, snout-vent length both 84 mm), and two *C. t. gracilis* (BYU 13559 and 13561, snout-vent length 70 and 71 mm. respectively) were skinned, hand cleaned of muscle tissue and then boiled for two hours. The skulls were then soaked in Clorox bleach at full strength for 35 minutes with adequate results. Care must be taken not to leave a skull too long in the bleach solution. If not properly attended, disarticulation occurs after a certain length of time depending on the size and thickness of the skull bones.

Myological studies were made on *C. t. septentrionalis* (BYU 31906-8, 31910, 31024 and 31925 with snout-vent lengths of 77, 84, 74, 92, 84 mm. respectively) and *A. u. parva* (BYU 14396, 14444, 14448-9 and 14453 with snout-vent lengths of 111, 108, 91, 75, and 127 mm. respectively). All specimens were carefully skinned and muscles dissected using small pieces of a new razor blade held securely in an x-acto knife handle. All specimens studied had been preserved in 10 percent formalin.

All drawings were made on Clearprint "fade-out" paper. The specimens were examined under a 10X-40X binocular dissecting scope and then drawn

in pencil using a micrometer eyepiece for exactness. The drawings were then enlarged by use of an opaque projector and inked using a L 4 Koh-I-Noor drawing pen. Stippling and line-shading methods described by Zweifel (1965) were adopted, using a #00 Koh-I-Noor drawing pen. Lettering was made with Prestype futura demi 18 and 36 point.

Photographs of all work accomplished were made for comparison purposes using an Exacta camera with an f22 aperture at 1/25 of a second and a double flash attachment. Expansion rings were used to obtain a 4:1 ratio enlargement. Kodak plus-X ASA 125 pan film was used.

OSTEOLOGY

An extensive study of all the skeletal elements of the body is not the primary purpose of this report. The discussion, therefore, is limited to the skull, wrist bones, and a comparison of the teeth. In each case, a full description of *A. u. parva* is given under each element using two skulls to determine all structures and listed as "A". This is followed by *only* the comparative differences noted in skulls of *C. t. septentrionalis* under each element and listed as "C". Two skulls each of *C. t. tigris* and *C. t. gracilis* were also examined for comparative purposes. If not otherwise stated, items not listed in "C" are essentially the same as those in "A".

General Description of the Skull

A. Generally, the skull can be considered heavily ossified for members of the family Teiidae having the dorsal surface rather rugose with prominent indentations present indicating positioning of overlying scutellation. Prominent dorsolateral orbital fenestrae dominate the middle portion of the skull. Posteriorly, two prominent fenestrae are present: a posterodorsal supratemporal fenestra and a posteroventral infratemporal fenestra separated by a temporal arch composed of the fused postorbital-postfrontal and the squamosal bones. Such a condition is termed diapsid and is typical of the condition seen in the fossil ancestors of modern lizards (Romer, 1966).

The foramina of the ventral surface anteriorly are those for the vomeronasal organs of Jacobson followed by the elongate internal nares. The floor of the orbit in the central portion of the skull is opened by the infraorbital foramen.

The occipital portion of the skull forms a posterior union for dorsal and ventral segments to enclose the brain. The occipital bones are highly fused and relatively difficult to differentiate. The brain case is composed of ventral projections of the parietal, anterior projections of the supraoccipital, exoccipital, and the basioccipital. The foramen magnum poster-

ocentrally is bordered by the supraoccipital dorsally, the basioccipital ventrally and the exoccipitals laterally. The occipital condyle is tripartite and is located on the posterior end of the basioccipital and the medioventral projections of the exoccipitals.

The large quadrate bones of the posterolateral portion of the ventral surface are loosely attached to the occipital processes and thus appear to allow for greater expansion of the lower jaw.

C. Generally, the skull is lighter, that is the bones are thinner and the dorsal surface is relatively glabrous. There is little indication of indentations for scutellation on the dorsal surface. The anteromedial border of the orbit is cartilaginous and the occipital portion of the skull is not highly fused, permitting more elements to be more easily distinguished.

More specifically, the differences between the two genera are considered with each of the individual skull elements.

Description of Skull Elements

All elements, for the sake of clarity, are discussed in alphabetical order. Only bones which are paired are indicated as such.

Basioccipital. (Fig. 2, 3, 5, and 6)

A. This bone is partially fused into the occipital complex. It forms the posteroventral border of the foramen magnum and extends anteriorly to articulate with the basisphenoid. It is bounded laterally by the exoccipitals and forms the floor of the brain case having fused anterolaterally with a pair of processes from the basisphenoid. Posteriorly, a pair of strongly developed basioccipital tuberosities can be seen which extend ventrally and slightly laterally. A slight median ridge extends along the suture line between the basioccipital and the exoccipitals.

C. The bone is thin on the ventral surface and the suture lines between it and the exoccipital are prominent.

Basisphenoid. (fig. 2, 3, 5, and 6)

A. This is the main bone of the floor of the cranium. It is bordered posteriorly by the basioccipital and anteriorly forms a forward projection which proceeds along the base of the brain called the rostral parasphenoid which we considered a separate element. Ventrally, articulation is with the pterygoid bone by means of two ventral foot-shaped basiptyergoid processes. Lateral extensions form an irregular suture with the basioccipitals. The dorsomedial portion forms the sella turcica.

C. Relatively little difference is noted.

Ectopterygoid.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. Posteriorly, it articulates with the anterolateral projection of the pterygoids. A prominent ectopterygoid process is noted as a ventral projection. Laterally, articulation is with the maxilla, jugal, and pterygoids, but a complete separation of jugal from the pterygoid or separation of maxilla from the jugal is made. Anteriorly, articulation is with the palatine bones. The medial border forms the lateral margin of the infraorbital foramen. Dorsally, it forms the posterolateral floor of the orbit.

C. The ectopterygoid process is pronounced and a separation of it from the pterygoid is complete, thus forming a small anterior border of the infratemporal fenestra.

Epipterygoid.—paired bones (Fig. 3 and 6)

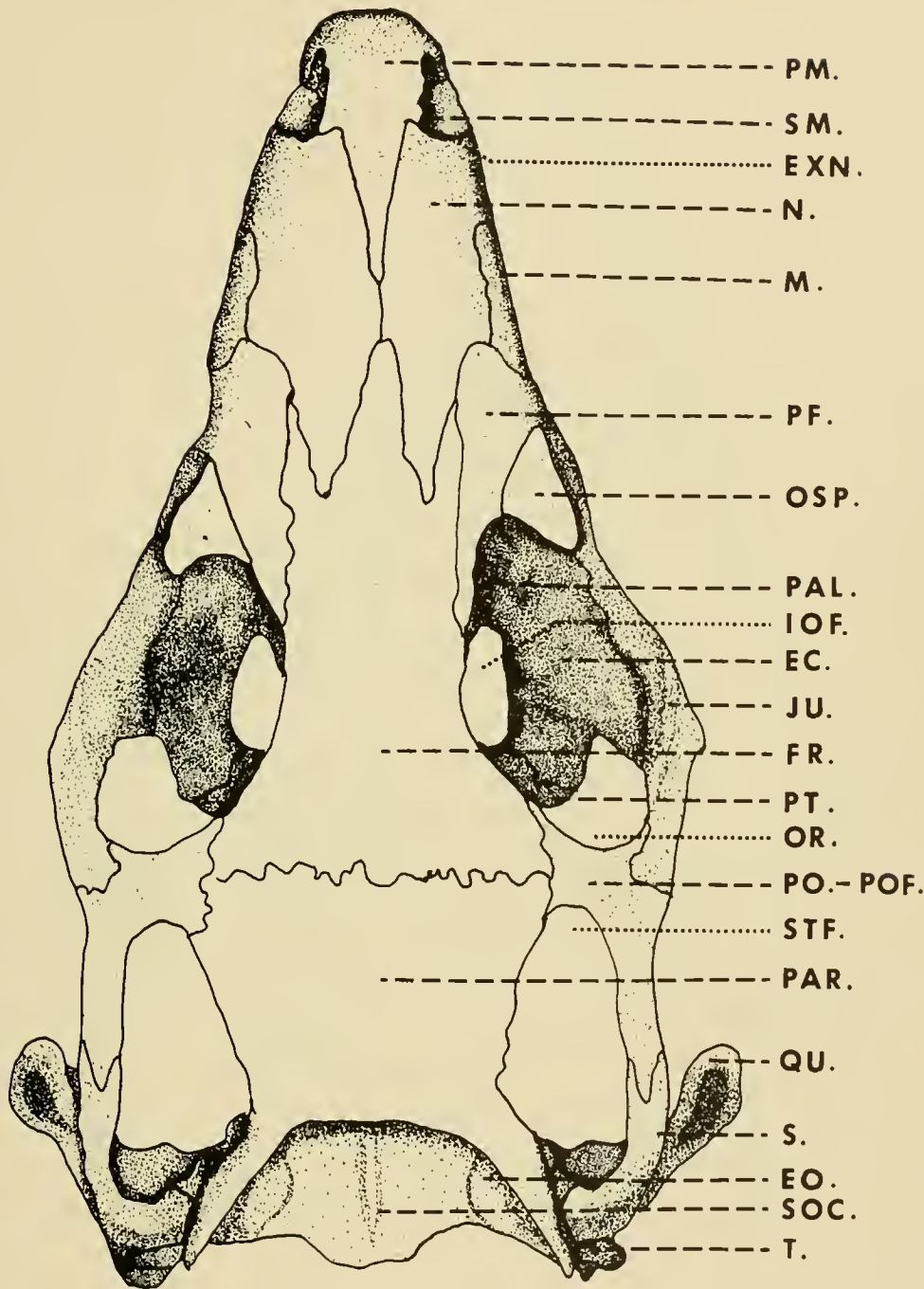
A. This pillar-shaped bone forms the anterolateral wall of the brain case. Articulation is with the pterygoid ventrally by means of a small depression and dorsally with an anteroventral projection of the parietal. A prominent lateral ridge is visible for its entire length.

C. Relatively little difference is noted.

Exoccipital.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. The limits of this bone are difficult to determine as there has been an extensive amount of fusion. Articulation sutures with the opisthotic were not located. The opisthotic, therefore, has been included in this description. Jollie (1960) concurred that sutures were not observable and Dubois (1943) called a part of this bone the otoccipital in *Cnemidophorus*. An extreme posterior projection of the exoccipital forms the lateral portion of the occipital condyle. Medially, it forms the posterolateral wall of the brain case. A large posterolateral paroccipital process extends to articulate with the tabular, parietal and quadrate. Ventral to the paroccipital process a portion of the membranous labyrinth is housed. The sutures separating the exoccipital from the prootic are not definite, but appear to be along the anterior margin of the paroccipital process. No young specimens were available in the collection to determine if this is but a function of age. The suture for articulation with the supraoccipital is lightly marked by a posterodorsolateral ridge extending from the foramen magnum anteriorly to the base of the parietal. Several foramina can also be noted on the posterolateral walls which include the foramen rotundum, two small hypoglossal foramina and the posterior border of the fenestra ovalis.

C. The paroccipital process articulates by means of a small cartilaginous projection with the posteromedial portion of the squamosal bone as well as articulating with the tabular, parietal, and quadrate. The suture lines for articulation with both the prootic and the supraoccipital bones are more distinct. The ridges denoting position of the semicircular canals are not as definite.

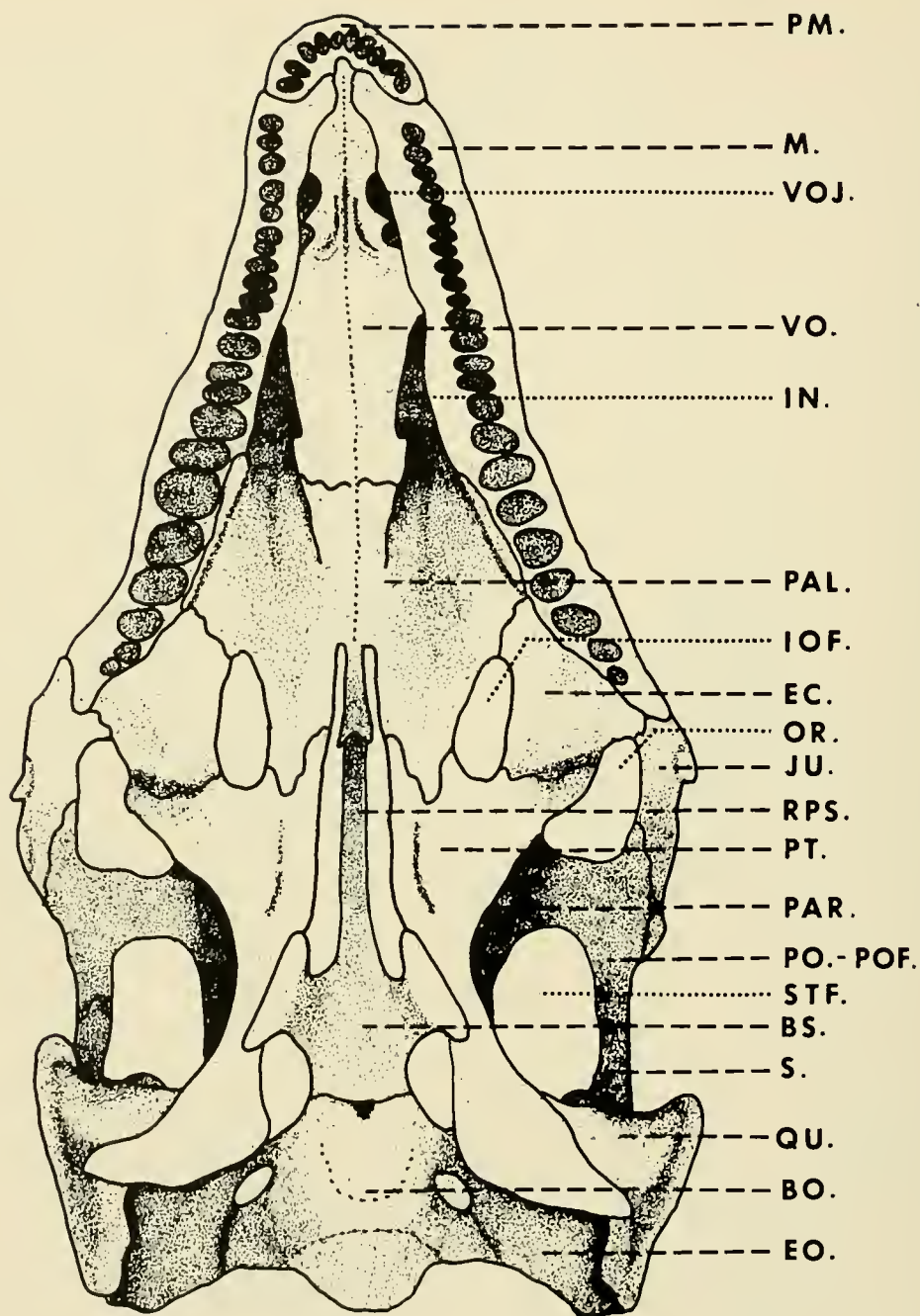


Skull Bones	
BO.	Basioccipital
BS.	Basisphenoid
EC.	Ectopterygoid
EO.	Exoccipital
EP.	Epipterygoid
FR.	Frontal
JU.	Jugal
LA.	Lacrimal
M.	Maxilla
N.	Nasal
OSP.	Os Palabrae

PAL.	Palatine
PAR.	Parietal
PF.	Prefrontal
PM.	Premaxilla
PO.-POF.	Postorbital-postfrontal
PR.	Prootic
PT.	Pterygoid
QU.	Quadrato
RPS.	Rostral Parasphenoid
S.	Squamosal
SM.	Septomaxilla
VO.	Vomer

Foramina of the Skull	
EXN.	External nares
IN.	Internal nares
IOF.	Infraorbital foramen
ITF.	Infratemporal fenestra
NF.	Nasal foramen
OR.	Orbital fenestra
SLF.	Supralabial foramen
STF.	Supratemporal fenestra
VOJ.	Vomero-nasal organs of Jacobson foramen

Fig. 1. Ameiva undulata parva. Dorsal view of skull. (6.2X)



Skull Bones

BO.	Basioccipital
BS.	Basisphenoid
EC.	Ectopterygoid
EO.	Exoccipital
EP.	Epipterygoid
FR.	Frontal
JU.	Jugal
LA.	Lacrima
M.	Maxilla
N.	Nasal
OSP.	Os Palabrae

PAL.	Palatine
PAR.	Parietal
PF.	Prefrontal
PM.	Premaxilla
PO.-POF.	Postorbital-postfrontal
PR.	Prootic
PT.	Pterygoid
QU.	Quadrate
RPS.	Rostral parasphenoid
S.	Squamosal
SM.	Septomaxilla
VO.	Vomer

Foramina of the Skull

EXN.	External nares
IN.	Internal nares
IOF.	Infraorbital foramen
ITF.	Infratemporal fenestra
NF.	Nasal foramen
OR.	Orbital fenestra
SLF.	Supralabial foramen
STF.	Supratemporal fenestra
VOJ.	Vomero-nasal organs of Jacobson foramen

Fig. 2. *Ameiva undulata parva*. Ventral view of skull. (6.2X)

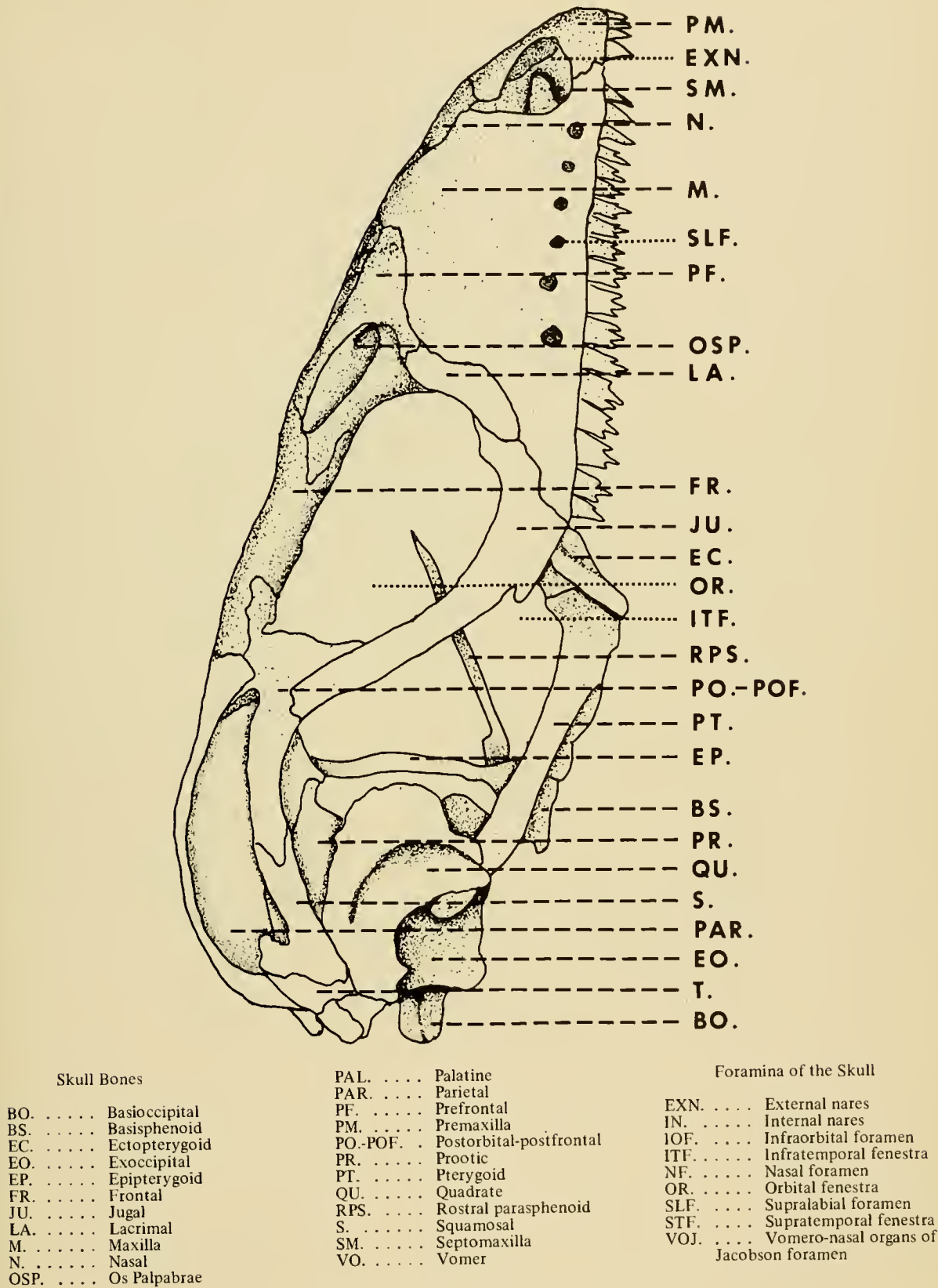
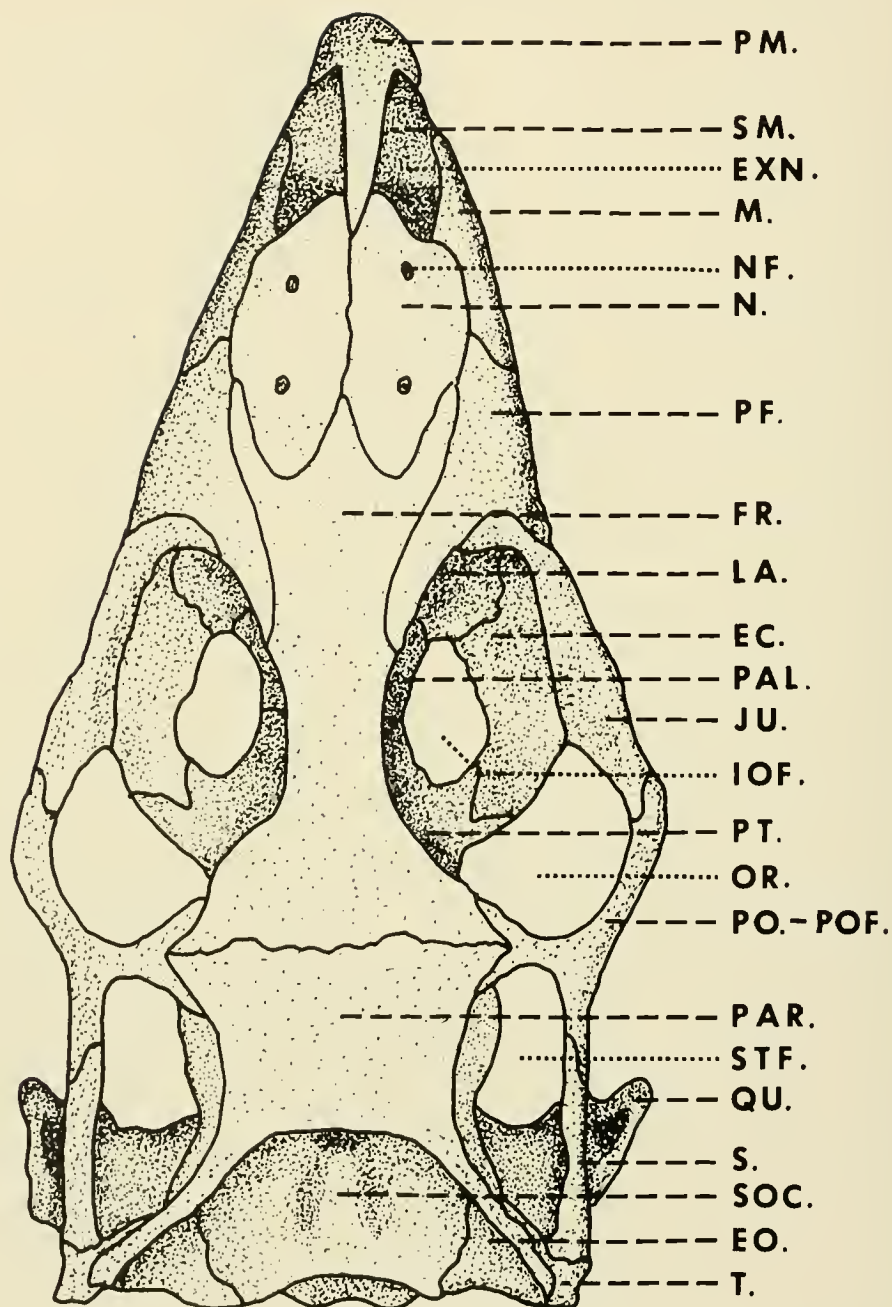


Fig. 3. *Ameiva undulata parva*. Lateral view of skull. (6.2X)



Skull Bones

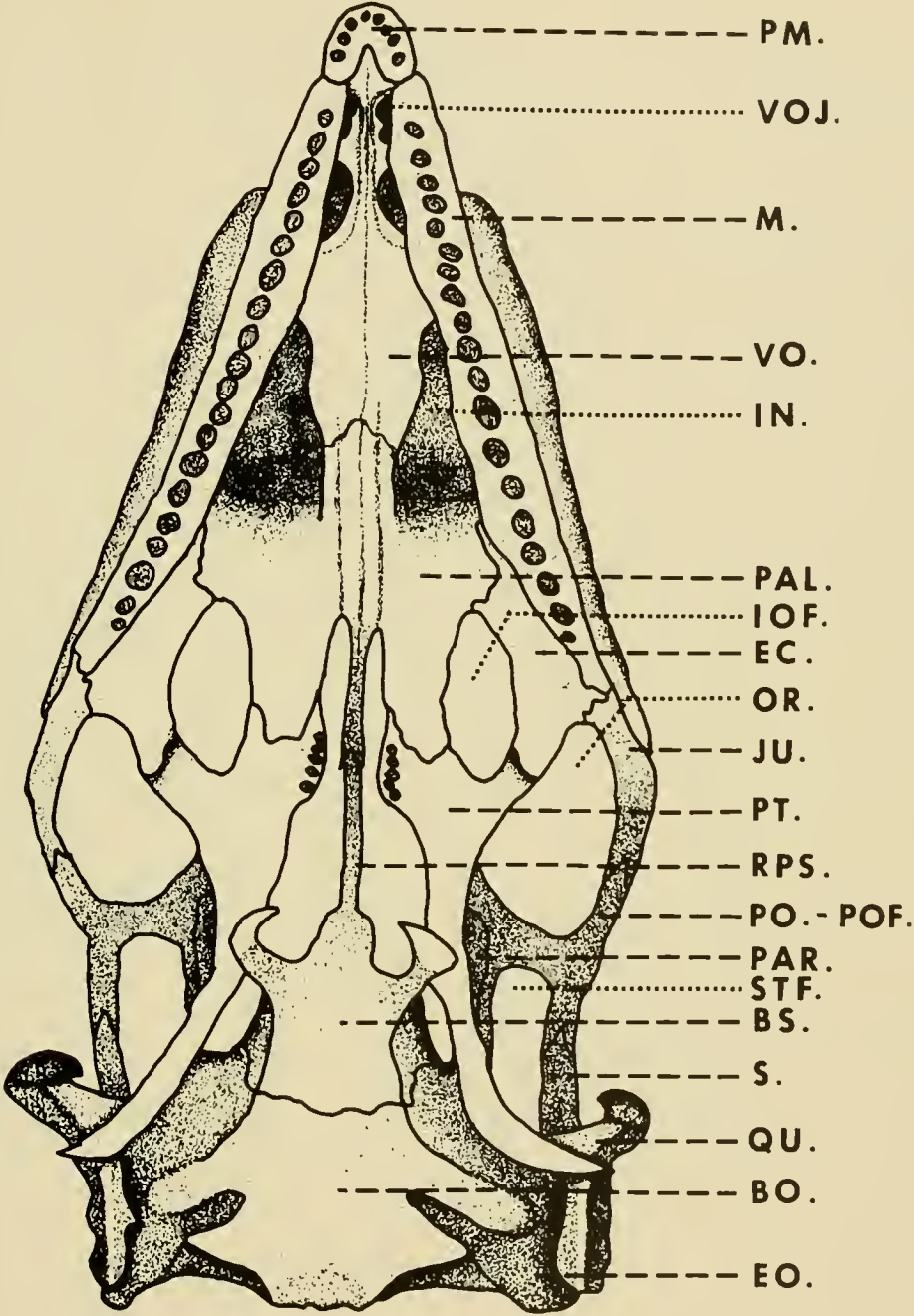
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BS.	Basisphenoid
EC.	Ectopterygoid
EO.	Exoccipital
EP.	Epipterygoid
FR.	Frontal
JU.	Jugal
LA.	Lacrimal
M.	Maxilla
N.	Nasal
OSP.	Os Palabrae

PAL.	Palatine
PAR.	Parietal
PF.	Prefrontal
PM.	Premaxilla
PO.-POF. .	Postorbital-postfrontal
PR.	Prootic
PT.	Pterygoid
QU.	Quadrate
RPS.	Rostral parasphenoid
S.	Squamosal
SM.	Septomaxilla
VO.	Vomer

Foramina of the Skull

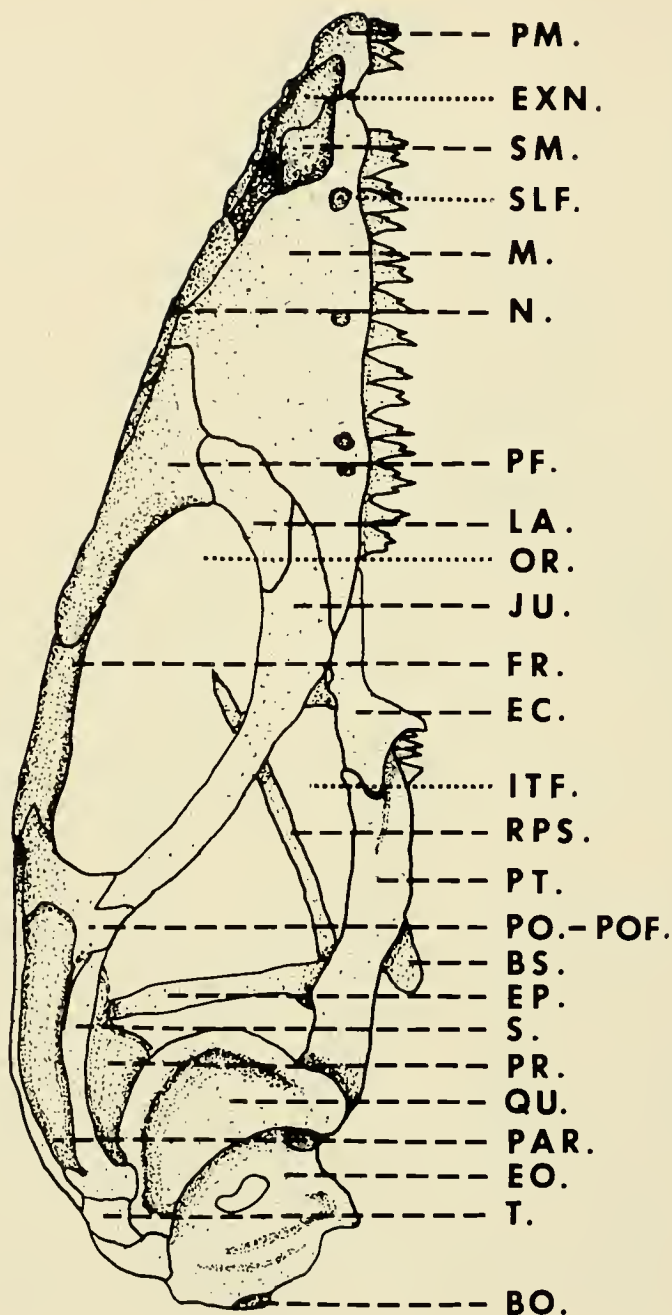
EXN.	External nares
IN.	Internal nares
IOF.	Infraorbital foramen
ITF.	Infratemporal fenestra
NF.	Nasal foramen
OR.	Orbital fenestra
SLF.	Supralabial foramen
STF.	Supratemporal fenestra
VOJ.	Vomero-nasal organs of Jacobson foramen

Fig. 4. *Cnemidophorus tigris septentrionalis*. Dorsal view of skull. (8.4X)



Skull Bones		Foramina of the Skull	
BO.	Basioccipital	EXN.	External nares
BS.	Basisphenoid	IN.	Internal nares
EC.	Ectopterygoid	IOF.	Infraorbital foramen
EO.	Exoccipital	ITF.	Infratemporal fenestra
EP.	Epipterygoid	NF.	Nasal foramen
FR.	Frontal	OR.	Orbital fenestra
JU.	Jugal	SLF.	Supralabial foramen
LA.	Lacrimal	STF.	Supratemporal fenestra
M.	Maxilla	VOJ.	Vomero-nasal organs of Jacobson foramen
N.	Nasal		
OSP.	Os Palabrae		
PAL.	Palatine		
PAR.	Parietal		
PF.	Prefrontal		
PM.	Premaxilla		
PO.-POF.	Postorbital-postfrontal		
PR.	Prootic		
PT.	Pterygoid		
QU.	Quadrate		
RPS.	Rostral parasphenoid		
S.	Squamosal		
SM.	Septomaxilla		
VO.	Vomer		

Fig. 5. Cnemidophorus tigris septentrionalis. Ventral view of skull. (8.4X)



Skull Bones

BO.	Basioccipital
BS.	Basisphenoid
EC.	Ectopterygoid
EO.	Exoccipital
EP.	Epipterygoid
FR.	Frontal
JU.	Jugal
LA.	Lacrimal
M.	Maxilla
N.	Nasal
OSP.	Os Palabrae

PAL.	Palatine
PAR.	Parietal
PF.	Prefrontal
PM.	Premaxilla
PO.-POF. .	Postorbital-postfrontal
PR.	Prootic
PT.	Pterygoid
QU.	Quadrate
RPS.	Rostral parasphenoid
S.	Squamosal
SM.	Septomaxilla
VO.	Vomer

Foramina of the Skull

EXN.	External nares
IN.	Internal nares
IOF.	Infraorbital foramen
ITF.	Infratemporal fenestra
NF.	Nasal foramen
OR.	Orbital fenestra
SLF.	Supralabial foramen
STF.	Supratemporal fenestra
VOJ.	Vomero-nasal organs of Jacobson foramen

Fig. 6. *Cnemidophorus tigris septentrionalis*. Lateral view of skull. (8.4X)

C. The middle portion is much narrower with the entire infraorbital foramina appearing visible in a dorsal view. The ventral portion of the frontal is deeply grooved, with prominent anterior arches noted. Of the three anterior processes, the lateral two are slightly longer than the central median process.

Frontal. (Fig. 1 and 3)

A. The dorsal surface of this bone is very rugose, possessing deep indentations for overlying scutellation. The posterior margin is buttressed by the parietal and posterolaterally articulation occurs with the anterior projections of the postorbital-postfrontal. The ventral surface is convex medially, tending to flatten posteriorly when seen in cross section. When viewed dorsally, the middle portion appears to extend laterally to cover the medial borders of the infraorbital foramina. Laterally, the dorsal margin of the orbit is formed. In the anterior aspect, three processes are produced of which the middle is the longest and inserts between the two nasal bones. The lateral processes insert between the nasals and the prefrontals. Ventrally, the anterior portion is arched into ventral columns to allow passage for the olfactory tracts. No pineal foramen is present.

Jugal.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. A long curved bone forming the ventrolateral margin of the orbit and the anterior margin of the infratemporal fenestra. Articulation posteriorly is with the ventral surface of the postorbital-postfrontal and ventrally a small projection articulates with the pterygoid posteriorly and the ectopterygoid anteriorly. The anterior-most border articulates with the lacrimal dorsally and the maxilla ventrally. A small spur is noted on the posterior margin of its ventral surface.

C. Ventrally, articulation is completely with the ectopterygoid and not with a portion of the pterygoid. No spur is noted on the posterior margin of the ventral surface.

Lacrimal.—paired bones (Fig. 3, 4, and 6)

A. Found in the anteroventral portion of the orbit, this bone articulates posteriorly with the jugal, ventrally with the maxilla and dorsally with the prefrontal. In the anteromedial aspect the lacrimal duct is found, but no part of the palatine canal is formed.

C. The dorsal-most portion of the palatine canal is formed by the lacrimal.

Nasal.—paired bones (Fig. 1, 3, 4, and 6)

A. The nasals form the anterodorsal portion of the rostrum and enter the extreme posterior border of the external nares. Posteriorly, separation is by the central process of the frontal. They then meet in the center for a short distance only to be separated anteriorly by the posterior projection of the premaxilla.

Posterolaterally, articulation is with the prefrontal, being separated from it on the extreme posterior margin by the lateral process of the frontal. Ventrally the dorsal surface of the nasal canal is formed and the dorsal surface is perforated by several irregularly spaced nasal foramina.

C. The central union of the two nasals is much longer and the nasal foramina seemingly are more regularly placed as well as having a larger posterior border where the external nares are formed.

Os palpebrae.—paired bones (Fig. 1 and 3)

A. This is a small triangular ossified bone in the anterodorsal border of the orbit which articulates entirely with the prefrontal.

C. The os palpebrae is not present as an ossified structure.

Palatine.—paired bones (Fig. 2 and 5)

A. The palatine articulates posteriorly with the pterygoid and anteriorly with the ectopterygoid and maxilla. The anterior-most articulation is with the vomer and then a central union is formed beneath two strong ridges of the primary palate with the other palatine. A strongly developed depression marks the dorsal and lateral surfaces of the nasal canal and internal nares. The medial border of the palatine canal is also formed.

C. The anterior medial processes are also joined beneath two strong ridges of the primary palate contrary to the findings of Dubois (1943).

Parietal. (Fig. 1, 3, 4, and 6)

A. The parietal is a rugose bone with deep indentations indicating overlying scutellation and is roughly rectangular in shape. Two large posterior projections form the parietal arch and articulates with the tabular, squamosal, and the paroccipital processes of the exoccipital. Anterolaterally, articulation is with the postorbital-postfrontal and the remainder of the anterior border buttresses the frontal. Large ventrolateral flanges deflect downward to enclose the posterodorsal portion of the brain and articulate with the supraoccipital, exoccipital, and the epipterygoid. Ventrally, there is no central ridge, but the posterior central margin contains a deep indentation which may hold a remnant of the synotic tectum of the chondrocranium.

C. A small median ridge is present on the ventral aspect of this bone which may partially fill the area of the central fissure of the brain. The dorsal surface is only lightly rugose posteriorly with the anterior portion essentially glabrous.

Postorbital-postfrontal.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. The postorbital and postfrontal of most

saurians appear to have fused into one bone, although there is a light fusion line marked on the dorsal median surface. This bone divides the orbit from the supratemporal fenestra and also has a posterior projection which forms part of the temporal arch dividing the supratemporal fenestra from the infratemporal fenestra. Dorsally, articulation is anteriorly with the frontal and posteriorly with the parietal. Ventrally, articulation is anteriorly with the jugal and posteriorly with the squamosal. A small flange is observable in the anterior central position.

C. The postorbital and postfrontal are completely fused with no evidence of suture lines. No small flange is observable in the anterior central position.

Prefrontal.—paired bones (Fig. 1, 3, 4, and 6)

A. The prefrontal lies anterolateral to the frontal and articulates with its posterodorsal surface. Anteromedially, articulation is with the nasals and laterally with the maxilla. Posterodorsally, articulation is with the os palpebrae. A small posteroventral projection contacts the lacrimal and ventrally this projection then articulates with the palatine. The posteroventrolateral aspect forms a portion of the lacrimal duct.

C. A small posteroventrolateral projection forms the dorsal portion of the palatine canal. There is no os palpebrae to articulate with the posterodorsal border.

Premaxilla. (Fig. 1, 2, 3, 4, 5, and 6)

A. The anterior-most bone of the skull, the premaxilla, inserts dorsally between the nasals for a short distance posteriorly. Medially it is broad and ventrally articulation is with the vomer and with the maxilla ventrolaterally. The dorsolateral margins form the medial border of the external nares and the nasal canal. The ventral surface bears 10 peglike pleurodont teeth.

C. The posterior projection extends a shorter distance between the nasals. On the ventral surface, 8 peglike pleurodont teeth are borne. Medially the bone is rather narrow and less massive than in A.

Prootic.—paired bones (Fig. 3 and 6)

A. The position of the prootic is highly indeterminate since most of the suture lines are indefinite. This bone forms part of the posteroventrolateral wall of the brain case and encloses the area of the anterior semicircular canal. Posteriorly, the anterior border of the fenestra ovalis is formed and anteroventrally a well developed ridge then proceeds to the base of the basiptyergoid process. Dorsally and anteriorly articulation is with the parietal and posteriorly with the supraoccipital and exoccipitals. Ventrally and posteriorly the basioccipital and anteriorly the basisphenoid meet. The central portion is dominated by a lateral flange anterior to the fenestra ovalis.

C. The suture lines are more readily definable, but

the positioning of the semicircular canals is more difficult to determine because the external ridges are less pronounced in the bone.

Pterygoid.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. A "Y" shaped bone on the ventral surface of the skull, the pterygoid articulates posteriorly with the quadrate and anteriorly with the palatine medially and the ectopterygoid laterally. The central portion forms the posterior border of the infraorbital foramen. Ventrally, articulation is with the basiptyergoid process which fits into an oblique groove on the ventral surface; on the dorsal surface directly opposite the basiptyergoid process, the epiptyergoid articulates in a small depression. The posteromedial margin is expanded into a knifelike ridge extending horizontally to the posterior end. Teeth are not present on the anteromedial portion. The lateral border, along most of its length, forms the medial edge of the infratemporal fenestra. The rostral parasphenoid rises dorsally between the pterygoids.

C. The anteromedial margin contains five pterygoid teeth. (Dubois, 1943, reported three on the pterygoid of *C. sexlineatus*.) The posteromedial margin is less expanded and the central gap between the two pterygoids is wider at the posterior margins.

Quadrate.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. The quadrate articulates with the articular of the lower jaw. The articulation is on cartilaginous pads thus allowing for greater jaw expansion. In the medial area, articulation is with the pterygoid posteriorly and anteriorly with the squamosal, tabular and paroccipital process of the exoccipital. The lateral border is expanded into a slightly recurved tympanic crest and the medial border also forms a small crest for loose articulation with the prootic. The union of the posterior margins of these two crests forms the seat of the middle ear.

C. The tympanic crest is not as greatly expanded laterally, but is highly recurved, thus forming an anterior tympanic recess.

Parasphenoid. (Fig. 2, 3, 5, and 6)

A. This is a long pointed foil-like projection proceeding anterodorsally from a fused position with the basisphenoid, between the two pterygoids, and rests beneath the lower surface of the brain. The parasphenoid is considered a separate element from the basisphenoid as its identity has been established embryologically, structurally, and paleontologically (Dubois, 1943).

C. Relatively little difference is noted.

Septomaxilla. (Fig. 3 and 6)

A. The septomaxilla is a thin plate extending from the vomer posterolaterally to the ventral margin of the maxilla with a small projection extending

anteriorly into the nasal canal.

C. Relatively little difference is noted.

Squamosal.—paired bones (Fig. 1, 2, 3, 4, 5, and 6)

A. The squamosal is a relatively simple bone flared posteriorly to articulate with the parietal, tabular, and narrowly with the quadrate. It forms the posterior half of the temporal arch separating the supratemporal fenestra from the infratemporal fenestra and articulates anteriorly with the postorbital-postfrontal

C. Relatively little difference is noted.

Supraoccipital. (Fig. 1 and 4)

A. Posteriorly, the supraoccipital forms the dorsal margin of the foramen magnum and anteriorly articulates with the parietal. Centrally, a ridge divides the bone into left and right halves. The lateral sutures with the exoccipital and the prootic are not distinct except for a small ridge which proceeds anterodorsally from the paroccipital process of the exoccipital dividing the supraoccipital from the prootic. The posterior end of the anterior semicircular canal and the medial end of the posterior semicircular canal enter anteriorly and unite.

C. The central ridge is not sharp, but the suture lines for the exoccipital and prootic are definable

Tabular.—paired bones (Fig. 1, 3, 4, and 6)

A. Posteriorly, the tabular inserts between the squamosal, quadrate, paroccipital process of the exoccipital and the posterior end of the parietal. Anteriorly, a small projection is sent forward along the ventral margin of the parietal arch for a short distance.

C. Relatively little difference is noted.

Prevomer.—paired bones (Fig. 2 and 5)

A. Medially, the prevomers exist as paired elements of the central anteroventral surface of the skull, joining the palatine posteriorly and anteriorly the maxilla and premaxilla on the ventral surface and the septomaxilla on the dorsal surface. Small foramina on the anterolateral edge mark the position of the vomeronasal organs of Jacobson and connect them with the nasal canal. Posterolaterally, the medial border of the nasal canal and external nares is formed. A small medial groove beginning centrally and proceeding posteriorly holds the beginning of what appears to be a cartilaginous support for the rostral parasphenoid.

C. Relatively little difference is noted.

Lower Jaw

A. The lower jaw is united anteriorly by a mental symphysis and posteriorly articulates with the quadrate. Each ramus is composed of six bones: the

angular, articular, coronoid, dentary, splenial and surangular. The articular makes almost a right angle with the angular, the anterior end of each ramus has a distinct lateral torsion (Fig. 7c), and the ventral surface is rugose. The dentary of each ramus bears a single row of pleurodont teeth, whereas the remaining bones are edentate. The prearticular is fused to the articular in the adult and will not be considered in this report as a separate element of the ramus.

C. The articular and the angular are essentially in a straight line. No lateral torsion is seen in the anterior end of the ramus (Fig. 8c). The ventral surface of the ramus is essentially glabrous.

Angular. (Fig. 7 and 8)

A. The angular is positioned at the posteroventral angle of the lower jaw. It articulates at almost right angles dorsomedially with the articular. Dorsolateral articulation is with the surangular. The element then extends forward where anterolateral articulation is with the dentary and anteromedial articulation is with the splenial. One small foramen, the angular foramen, is located on the medial surface.

C. The articulation of the angular and the articular is essentially a straight line.

Articular. (Fig. 7 and 8)

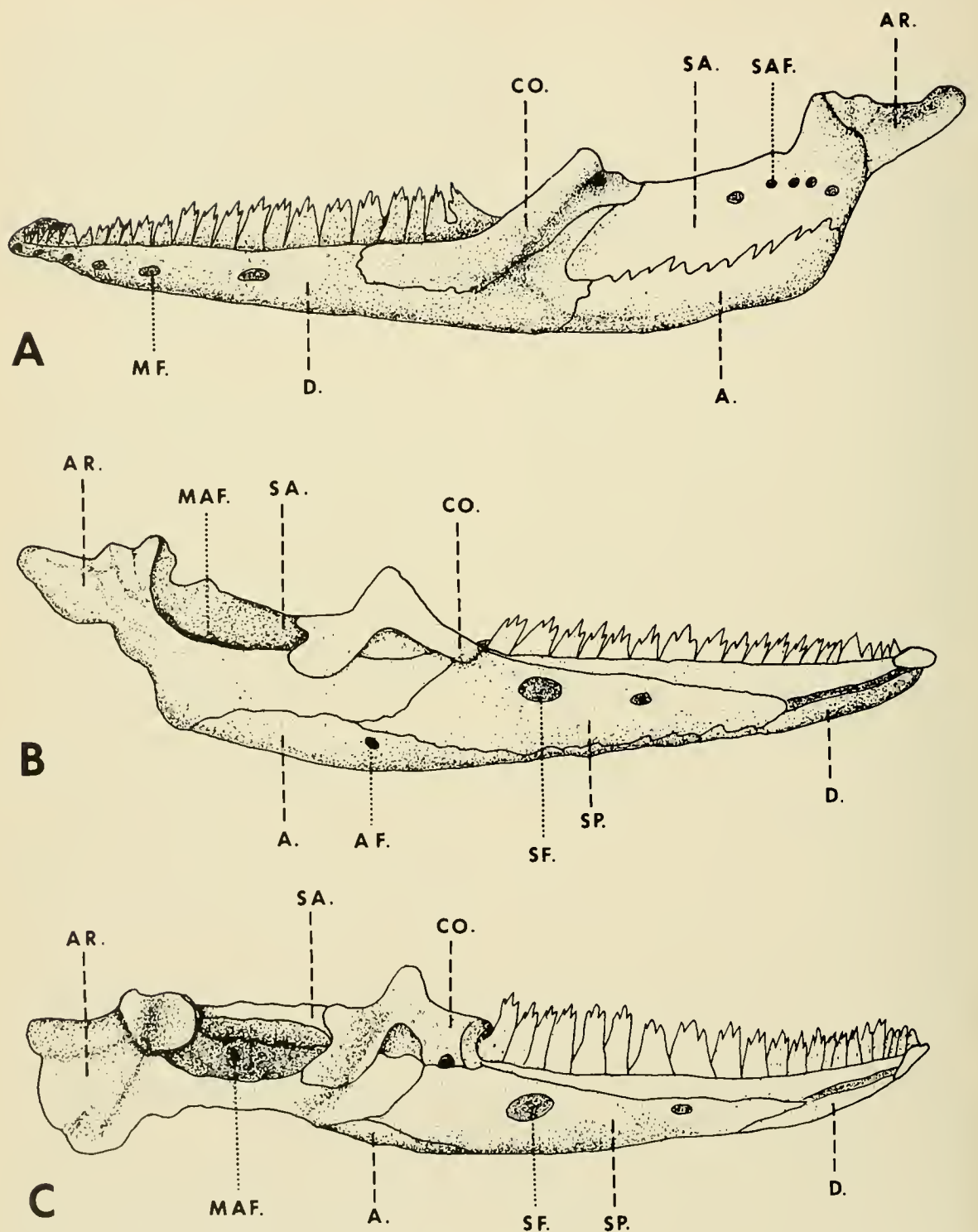
A. This is the posterior-most bone of the ramus. Fusion with the prearticular is so complete that separate elements are not detectable in the adult. The articulating surface for the quadrate on the anterodorsal margin is somewhat fused with the surangular so that suture lines are determined only with difficulty. The retroarticular process of the posterior edge is winglike and extends medially in the horizontal plane. Posteriorly, articulation is with the surangular dorsally and the angular ventrally. The element then extends forward along the medial surface to meet the ventromedial surface of the coronoid. There is articulation with the extreme posterior extension of the dentary and also the splenial. The inner aspect forms the posteromedial border of the large mandibular foramen.

C. The suture line between this bone and the surangular is more distinct. The retroarticular process extends in a ventrally projecting oblique plane.

Coronoid. (Fig. 7 and 8)

A. The coronoid is the central bone of the ramus, articulating posteriorly with the articular medially and the surangular laterally and forming posterocentrally and the anterior border of the mandibular foramen. Anteriorly, articulation is with the splenial and the dentary. On the medial surface, an arch over a small posterior extension of the dentary is formed as well as a large coronoid process dorsally.

C. The coronoid process is much sharper and possesses a small posteriorly directed hook.



A. Lateral view.
B. Medial view.
C. Dorsal view.

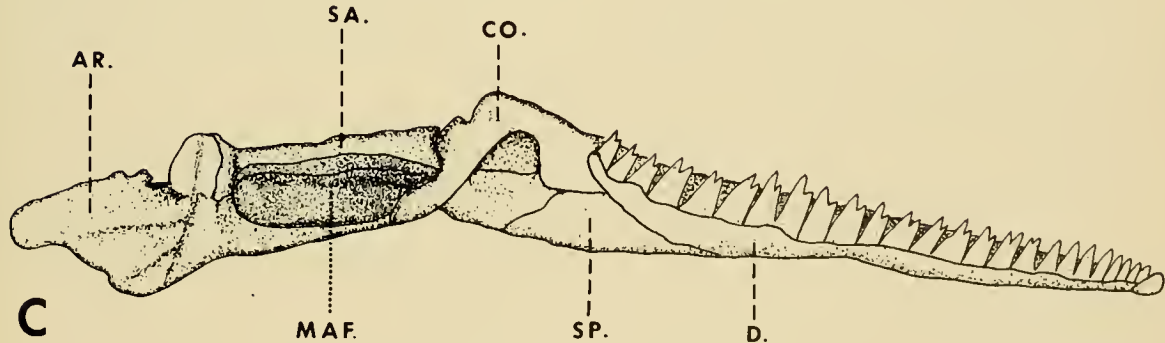
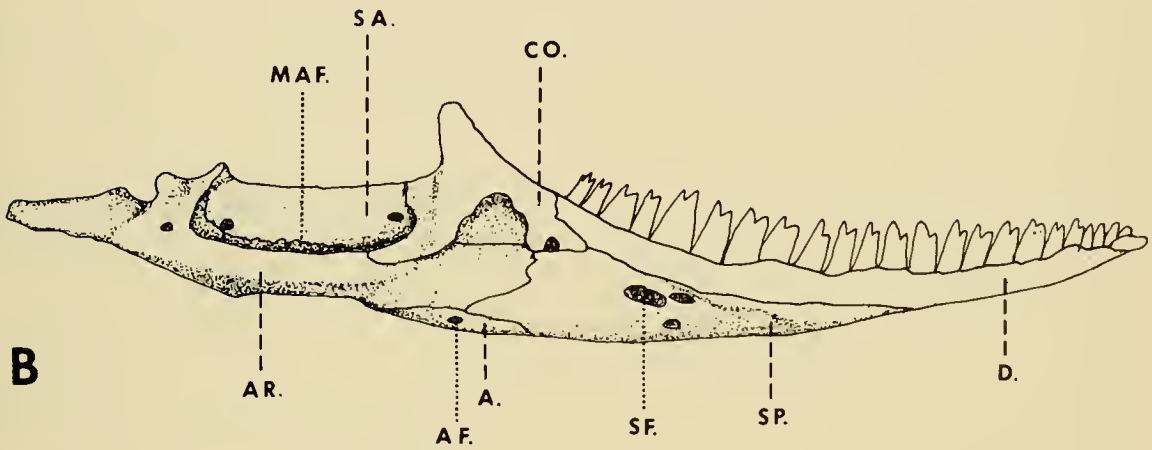
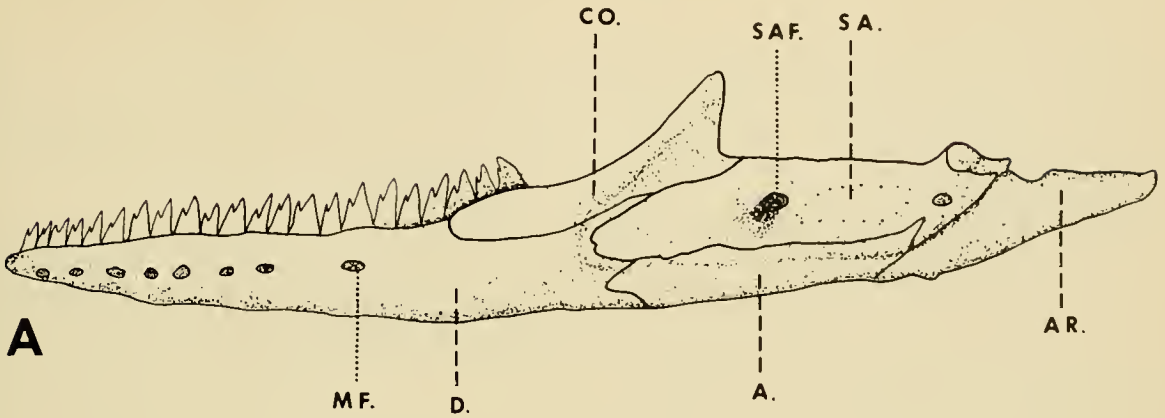
Foramina of the Lower Jaw

AF. Angular foramen
MAF. Mandibular foramen
MF. Mental foramen
SAF. Surangular foramen
SF. Splenic foramen

Lower Jaw Bones

A. Angular
AR. Articular
CP. Coronoid
D. Dentary
SA. Surangular
SP. Splenic

Fig. 7. *Ameiva undulata parva*. Lower Jaw. (4.9X)



A. Lateral view.
B. Medial view.
C. Dorsal view.

Foramina of the Lower Jaw

AF. Angular foramen
MAF. Mandibular foramen
MF. Mental foramen
SF. Splénial foramen
SAF. Surangular foramen

Lower Jaw Bones

A. Angular
AR. Articular
CP. Coronoid
SA. Surangular
D. Dentary
SP. Splénial

Fig. 8. *Cnemidophorus tigris septentrionalis*. Lower Jaw. (7.5X)

Dentary. (Fig. 7 and 8)

A. The dentary is the tooth-bearing bone and comprises the entire anterior half of each ramus. Union is made anteriorly by means of a mandibular symphysis with the dentary of the other ramus. Articulation is medially with the splenial, dorsally with the coronoid, posteriorly with the angular and postero-dorsally by means of a projection with the surangular. A dorsal projection proceeds posteriorly beneath the anterior process of the coronoid and unites under the coronoid arch with the articular. On the dorsal surface, there are 23 to 24 pleurodont teeth. Beneath the splenial on the medial surface, the Sulcus Cartilaginis Meckelii is found with a small Meckel's groove proceeding anterior to this sulcus to the mandibular symphysis. On the anterolateral surface, approximately six irregularly placed mental foramina are located.

C. The Meckel's groove proceeding anterior from the Sulcus Cartilaginis Meckelii to the mandibular symphysis is more ventrally placed and there are eight fairly evenly spaced mental foramina found along the lateral surface.

Splenial. (Fig. 7 and 8)

A. The splenial is found entirely on the medial surface of the ramus and articulates anteriorly with the dentary along most of its length. Posteriorly, articulation proceeds from dorsal to ventral with the coronoid, articular, and angular. One large foramen and one or perhaps two small splenial foramina are evident. This bone covers the area of the Sulcus Cartilaginis Meckelii.

C. Relatively little difference is noted.

Surangular. (Fig. 7 and 8)

A. The surangular forms the posterolateral wall of the ramus and articulates anteriorly from dorsal to ventral with the coronoid, dentary, and angular. The angular then proceeds along the ventral surface to the posterior end where articulation is with the articular. There are one large and two to six small surangular foramina found along the upper half of the bone. The surangular forms the lateral wall of the mandibular foramen.

C. There are only two foramina, one large and one small, located in the surangular.

Foramina of the Skull and Lower Jaw

In all cases, the foramina are considered comparatively in alphabetical order and positioning of margining elements is from anterior to posterior, from dorsal to ventral, or lateral to medial as the case applies.

Angular Foramen. (Fig. 7 and 8)

A. The angular foramen is located entirely within the angular.

C. No difference.

External nares. (Fig. 1, 3, 4, and 6)

A. The external naris is surrounded by the premaxilla, nasal, and maxilla and is found at the anterior end of the rostrum.

C. No difference.

Foramen magnum. (Not Figured)

A. The foramen magnum is the posterior-most foramen of the skull. It is bounded by the supraoccipital, occipitals, and basioccipital. The lower border forms a tripartite occipital condyle composed of a medial projection from each exoccipital and ventrally from a posterior projection of the basioccipital.

C. No difference.

Fenestra ovalis. (Not figured)

A. The fenestra ovalis is formed by the prootic and exoccipital bones and lies anterior to the paroccipital process.

C. No difference.

Fenestra Rotundum. (Not figured)

A. The fenestra rotundum is formed by the prootic and exoccipital and lies ventral to the fenestra ovalis.

C. No difference.

Hypoglossal foramen. (Not figured)

A. The hypoglossal foramen is found on the posteroventral side of the skull lateral to the occipital condyles and entirely within the exoccipital.

C. No difference.

Internal nares. (Fig. 2 and 5)

A. The internal nares are in the anteroventral surface of the skull and are surrounded by the maxilla, palatine, and vomer. They form directly posterior to the vomeronasal organs of Jacobson.

C. No difference.

Infraorbital foramen. (Fig. 1, 3, 4, and 6)

A. The infraorbital foramen is surrounded by the palatine, ectopterygoid, and pterygoid and lie on the anteroventral surface of the skull posterior to the internal nares.

C. No difference.

Infratemporal fenestra. (Fig. 3 and 6)

A. This is the large fenestra of the posterolateral margin of the skull. The edges are formed by the jugal, postorbital-postfrontal, squamosal, pterygoid, and quadrate bones.

C. The ectopterygoid bone enters the anterolateral margin.

Lacrimal foramen. (Not figured)

A. The lacrimal foramen is formed from the lacrimal and prefrontal to allow passage of the lacrimal canal.

C. No difference.

Mandibular foramen. (Fig. 7 and 8)

A. This is the large foramen of the posterodorsal surface of each ramus. It is formed from the coronoid, surangular, and articular.

C. No difference.

Mental foramina. (Fig. 7 and 8)

A. There are six irregularly spaced foramina of the lateral surface of each dentary bone.

C. There are usually eight regularly spaced foramina on each dentary bone.

Nasal foramina. (Fig. 8)

A. Usually, 0-1 foramen are found in the anterior end of the nasal.

C. Usually, 1-2 foramina are contained in the nasal bone.

Orbital fenestra. (Fig. 1, 2, 3, 4, 5, and 6)

A. The orbital fenestra is located dorsally in the central portion of the skull and is formed by the prefrontal, os palpebrae, frontal, postorbital-postfontal, lacrimal, and jugal.

C. No os palpebrae is found on the anteriomedial border.

Palatine canal. (Not figured)

A. Located ventral to the lacrimal foramen, this canal is formed by the lacrimal, palatine maxilla, and pterygoid. A small arch exists internally which appears to belong entirely to the maxilla. (Definite determination necessitates sectioning.)

C. A lateral projection of the prefrontal enters the margin of the canal.

Splenic foramina. (Fig. 7 and 8)

A. Located entirely within the splenic are two foramina, one large and one small.

C. There are three foramina, one large and usually two small, all within the splenic

Surangular foramina. (Fig. 7 and 8)

A. Several foramina occur along the dorsal portion of the surangular bones. These usually consist of one large and 2-6 small foramina.

C. Normally only one large foramen and one small foramen are found in the surangular.

Supralabial Foramina. (Fig. 3 and 6)

A. The supralabial foramina consist of approximately six small regularly spaced foramina on the lateral margin of the maxilla, positioned directly beneath the

supralabial scales.

C. The foramina are usually irregularly spaced and number four or five on each side.

Supratemporal fenestra. (Fig. 1, 2, 4, and 5)

A. This is the large posterodorsal fenestra of the skull and is formed by the squamosal, parietal and tabular.

C. No difference.

Vomeronasal foramina. (Fig. 2 and 5)

A. The vomeronasal foramina are small, usually three in number, and lie on the anteroventral surface of the skull on each side of the midline. Housed in the vomer and bordered by the maxilla, they serve for olfaction entrants by the tongue to the vomeronasal organs located within the nasal canal.

C. No difference.

Teeth**Dentary teeth. (Fig. 9a and 9c)**

A. The teeth are of pleurodont type with succession occurring throughout life by receiving replacement teeth which project into the base of the hollow, thinwalled old tooth. There are 22-23 teeth with the first 5 containing no accessory cusps. Beginning about tooth 6, there is a small anterior accessory cusp and, about tooth 9, a posterior accessory cusp. Both of these accessory cusps continue posteriorly to the last tooth.

C. The teeth also number 22-23, but only the first 4 are peglike (without accessory cusps). Beginning with tooth 5, a small anterior accessory cusp occurs and at tooth 20, the posterior accessory cusp is added.

Maxillary and Premaxillary teeth. (Fig. 9b and 9d)

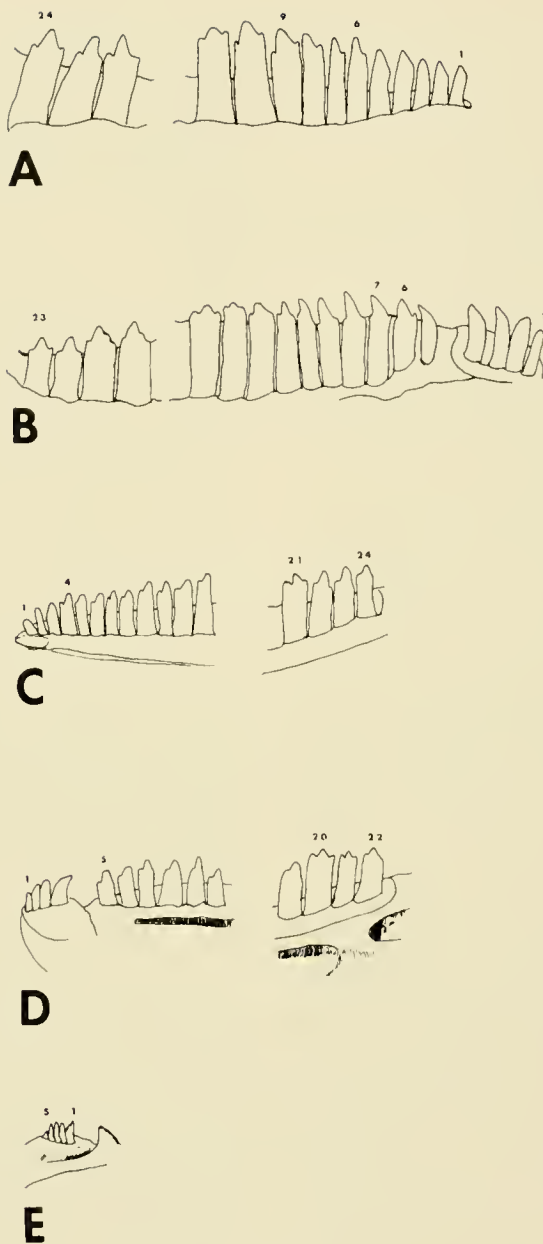
A. The teeth of the premaxilla and maxilla are of the same type as those of the dentary. Only the lateral four of the premaxilla are figured. The premaxilla bears 10 peglike teeth, the maxilla 18-21 teeth. The first maxillary tooth is peglike, but the second (6 in the figure) has an anterior accessory cusp. The third (7 in the figure) contains a posterior accessory cusp and both cusps are retained posteriorly to the last tooth (23 in the figure).

C. There are 8 peglike teeth on the premaxilla. The first tooth of the maxilla (5 in the figure) bears an anterior accessory cusp and the sixteenth (20 in the figure) adds a posterior accessory cusp. The last tooth (22 in the figure) may or may not possess the posterior accessory cusp.

Pterygoid teeth. (Fig. 93)

A. No pterygoid teeth were found.

C. There are five small peglike teeth occurring medially in the central portion of the pterygoid.



A. Dentary teeth. (7.OX)
 B. Maxillary and Premaxillary teeth. (5.8X)
Chemidophorus tigris septentrionalis. Teeth.
 C. Dentary teeth. (11.OX)
 D. Maxillary and Premaxillary teeth. (9.7X)
 E. Pterygoid teeth. (20.0X)

Fig. 9. *Ameiva undulata parva*. Teeth.

Wrist

The wrist of most teiids seems to consist of 8 or 9 carpal bones including carpals 1-5, a radiale, a proximal central, an ulnare, and an intermedium which may or may not be present. Each of the separate elements is fully described by Avery and Tanner (1964), so the discussion is here limited to the highly variable member of the carpal elements for the family Teiidae — the intermedium.

Stokely (1950) indicated that although this bone is highly characteristic of the lower tetrapods, particularly the amphibians, extinct reptiles and turtles, its presence is highly variable in several saurian families. One of these is the family Teiidae. He found the intermedium absent in *Cnemidophorus perplexus*, *C. melanostethus*, *Ameiva ameiva praesignis*, *Bachia intermedia*, and *Ophiognomon abendrothi*; but present in *Cnemidophorus gularis*, *C. hyperythrus beldingi*, and *C. t. tessellatus*. This extended the list of Camp (1923) for the family Teiidae which included an intermedium in *Tupinambis nigropunctatus*, *Tejus teguixin* and *Ameiva vulgaris*.

Because of the apparent differences within the genus *Ameiva* and the genus *Cnemidophorus*, those specimens of these two genera accessioned in the Vertebrate Natural History Museum at Brigham Young University were X-rayed and the radiographs carefully studied by means of a slide projector with the following results obtained for the specific individual specimens studied: 1. Intermedium present in *C. c. communus*, *C. burti*, *C. sexlineatus*, *A. u. parva*, *A. u. hartwegi*, and *A. u. sinistra*. 2. Intermedium absent in *C. t. tigris*, *C. t. septentrionalis*, *C. gularis*, and *A. auberi*. 3. The presence of the intermedium is questionable in *C. t. gracilis*, *C. t. canus*, *C. t. aethiops*, *C. exsanguis*, *C. d. deppei*, *C. l. lineatissimus*, *C. hyperythrus*, and *C. lemniscatus*.

MYOLOGY

The determination of muscles and the naming of them according to priority is difficult in the reptiles because of extreme variability as well as a lack of agreement upon homologies. For the most part, names were here chosen which were of the oldest origin as long as the muscle fit the general description of the original author. Where this was not possible, descriptive terminology for naming was applied. The deep skull musculature is not described here because Poglayen-Neuwall (1954) has a very detailed account of greater accuracy than was possible with the technique used in this report. These muscles include the levator bulbi dorsalis, levator bulbi ventralis, levator pterygoidei, protractor pterygoidei, pseudotemporalis profundus, and pseudotemporalis superficialis (Poglayen-Neuwall, 1954: Figs. 16, 9B).

Muscles are named in alphabetical order rather than by groupings into body areas in order to facilitate cross-reference with the figures. Comparative descriptions are listed the same as in the osteology section with A. indicating the five specimens of *Ameiva undulata parva* and "C." representing the six specimens of *Cnemidophorus tigris septentrionalis* observed.

M. Adductor Mandibulae Externus Medius. (Fig. 10, 16, and 17) Poglayen-Neuwall (1954).

A. The fibers of this muscle originate from the medial surface of the squamosal, the posterolateral parietal projection, the dorsolateral beveled surface of the parietal, and from the anterior and dorsal surfaces of the quadrate. The fibers extend anteroventrally with the dorsal ones more anteriorly directed. The insertion is along the dorsomedial surface of the surangular and the posterior surface of the coronoid. The body of the muscle fills the supratemporal fenestra and lies immediately medial to the adductor mandibularis externus superficialis and dorsolateral to the adductor mandibularis externus profundus from which it is only faintly separable.

C. Little difference is noted.

M. Adductor Mandibulae Externus Profundus. (Fig. 17 and 18) Poglayen-Neuwall (1954).

A. The muscle originates from almost the entire posteromedial border of the posterolateral projection of the parietal, from the paroccipital process of the exoccipital and from the dorsolateral surface of the posterior process of the prootic. The muscle then turns ventrally to enter the infratemporal fenestra and insert on the posterior surface of the coronoid. The muscle mass is not clearly separable from the adductor mandibularis externus medius in the dorsolateral position.

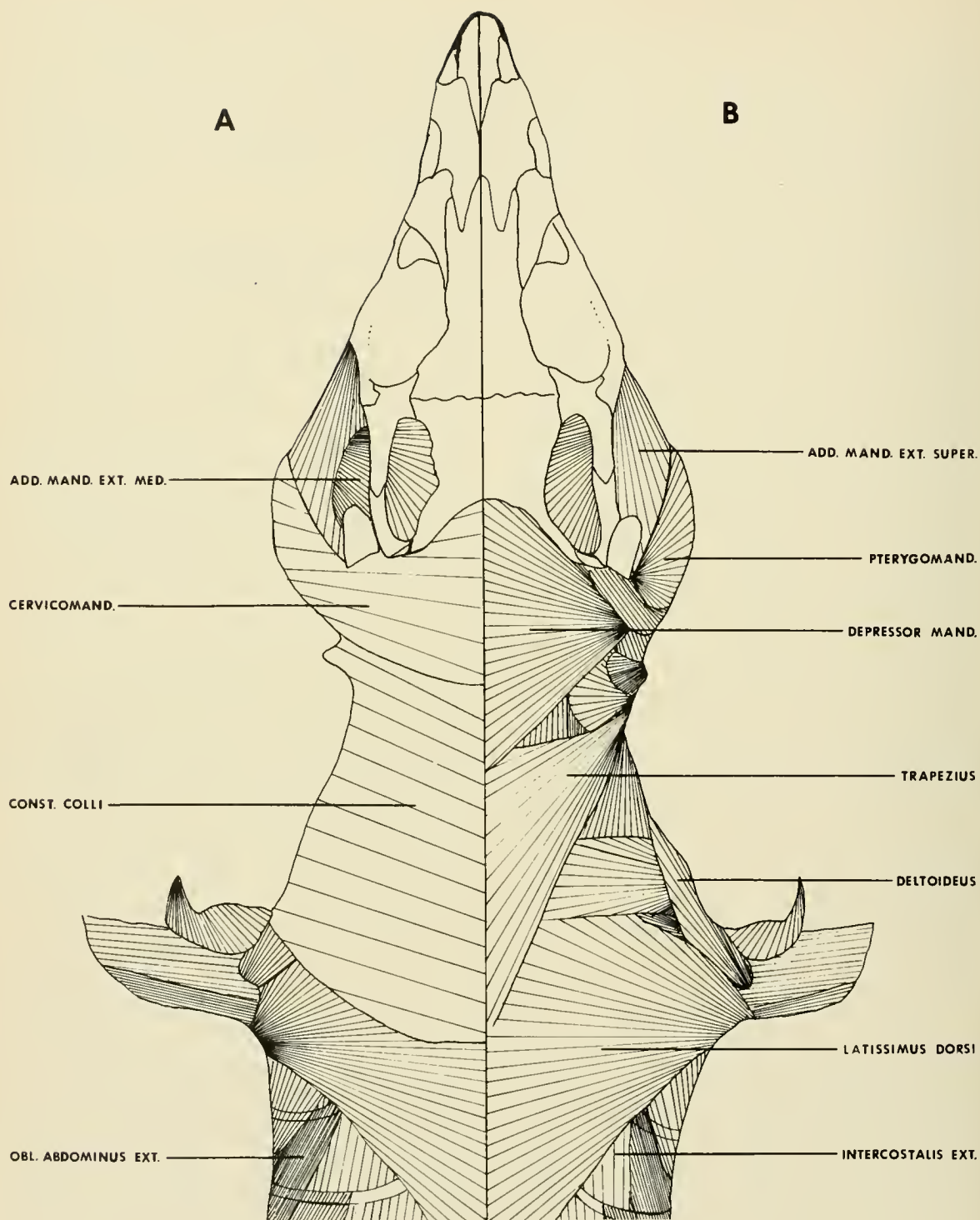
C. Little difference is noted.

M. Adductor Mandibularis Externus Superficialis. (Fig. 10, 16, 17) Poglayen-Neuwall (1954).

A. The origin is from the ventral surfaces of the postorbital-postfrontal, squamosal, a portion of the jugal and from the dorsal and anterior surface of the tympanic crest. The fibers of the muscle then extend anteroventrally to insert along the depressed lateral surface of the surangular with the more anterior fibers inserting on the lateral and posterolateral surfaces of the coronoid and the lateral surface of the angular. The body of the muscle fills the greater portion of the infratemporal fenestra with the medial portion scarcely distinguishable from the adductor mandibulae externus medius.

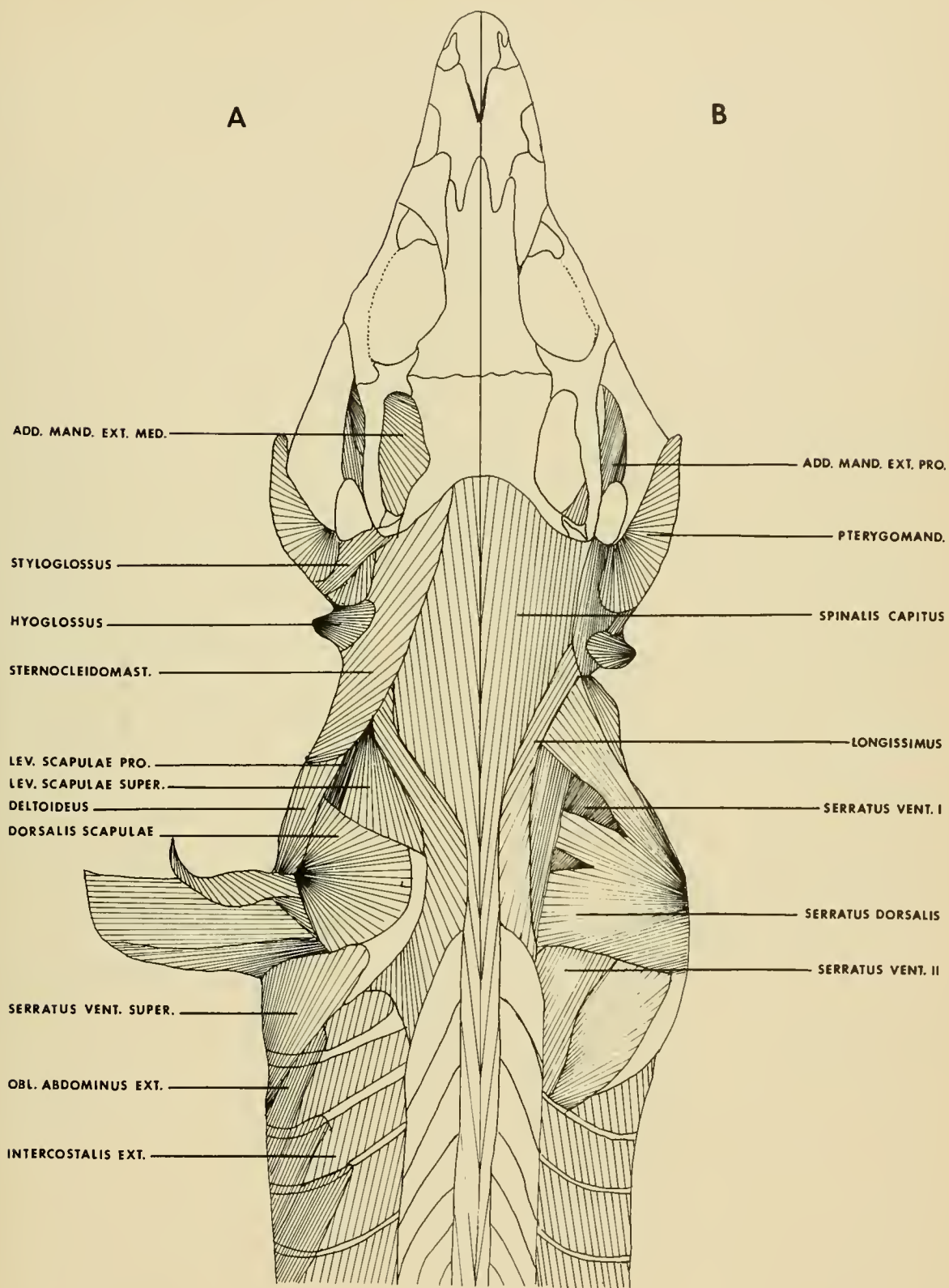
C. Little difference is noted.

M. Adductor Mandibulae Posterior. (Fig. 17 and 18) Poglayen-Neuwall (1954).



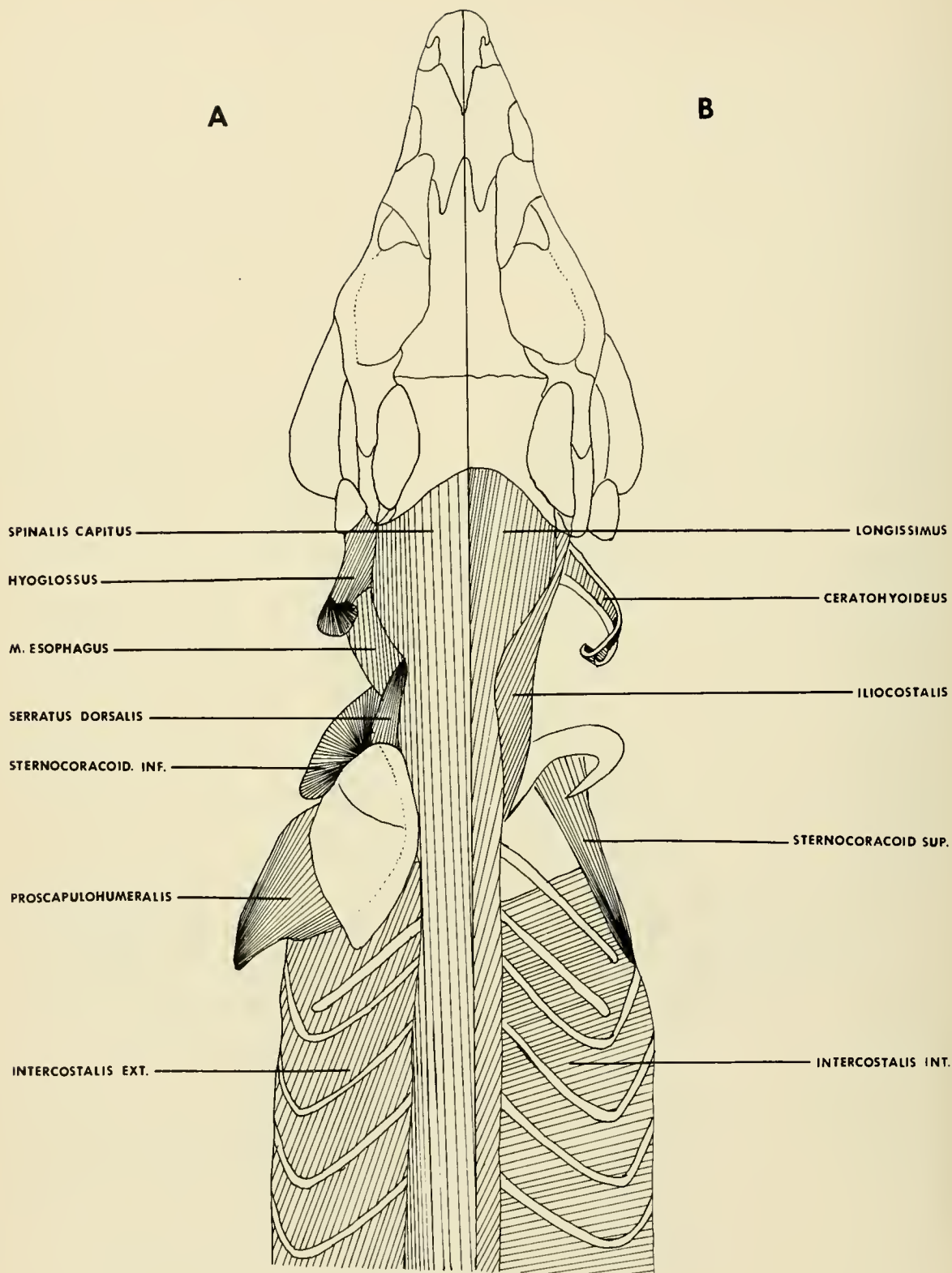
A. Superficial depth.
B. First depth.

Fig. 10. *Ameiva undulata parva*. Musculature dorsal view. (2.9X)



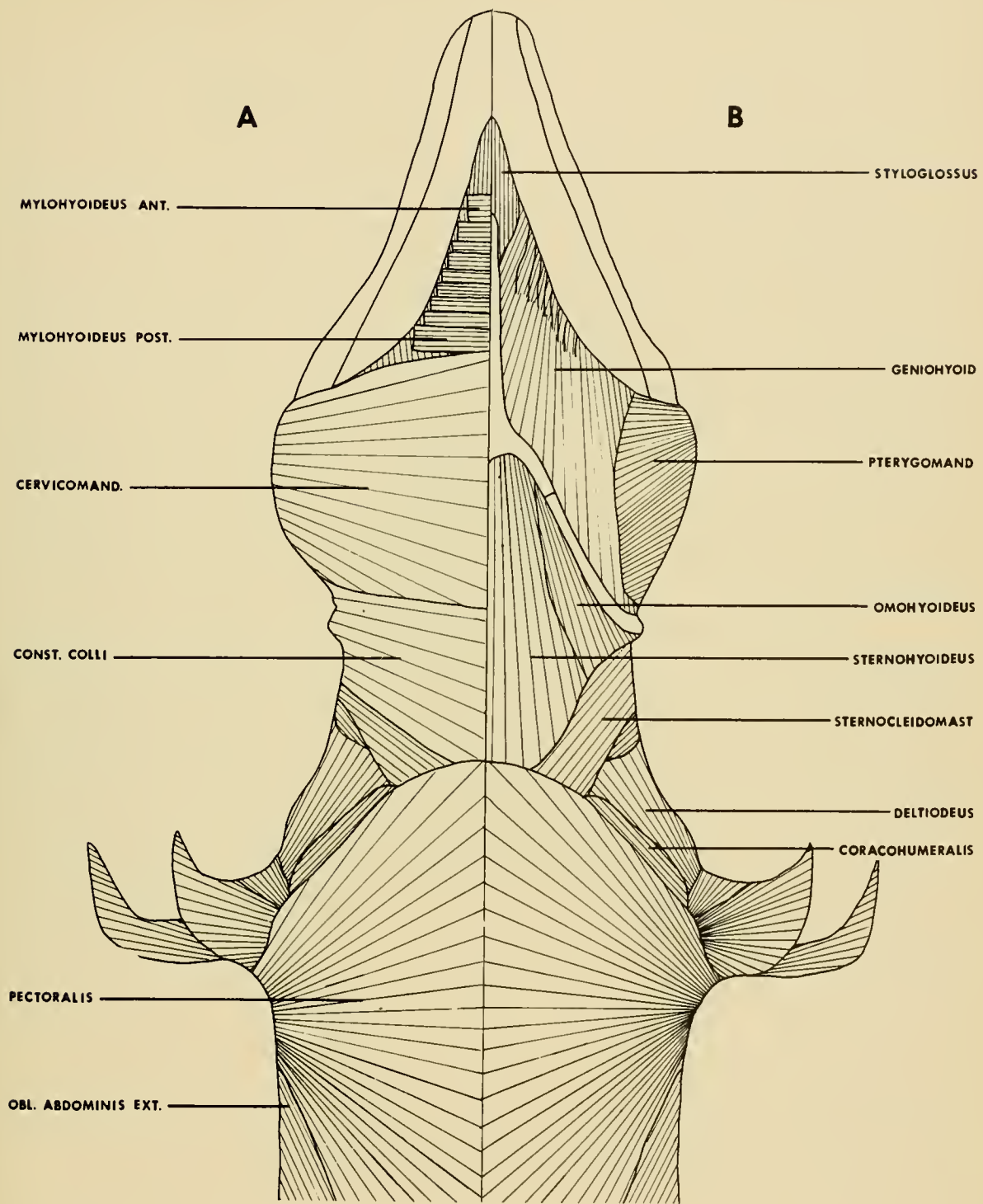
A. Second depth.
B. Third depth.

Fig. 11. *Ameiva undulata parva*. Musculature dorsal view. (2.9X)



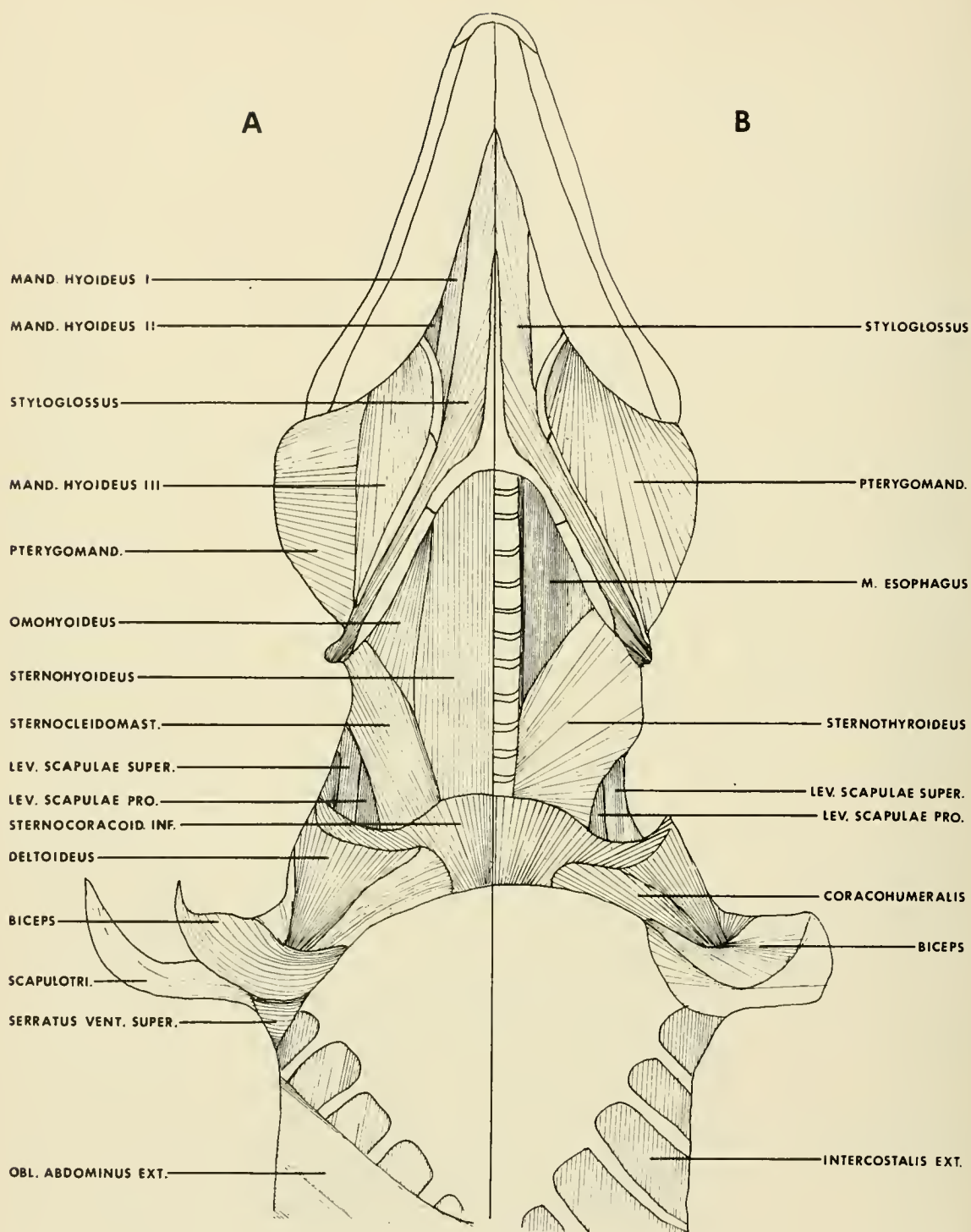
A. Fourth depth.
B. Fifth depth.

Fig. 12. *Ameiva undulata parva*. Musculature dorsal view. (2.9X)



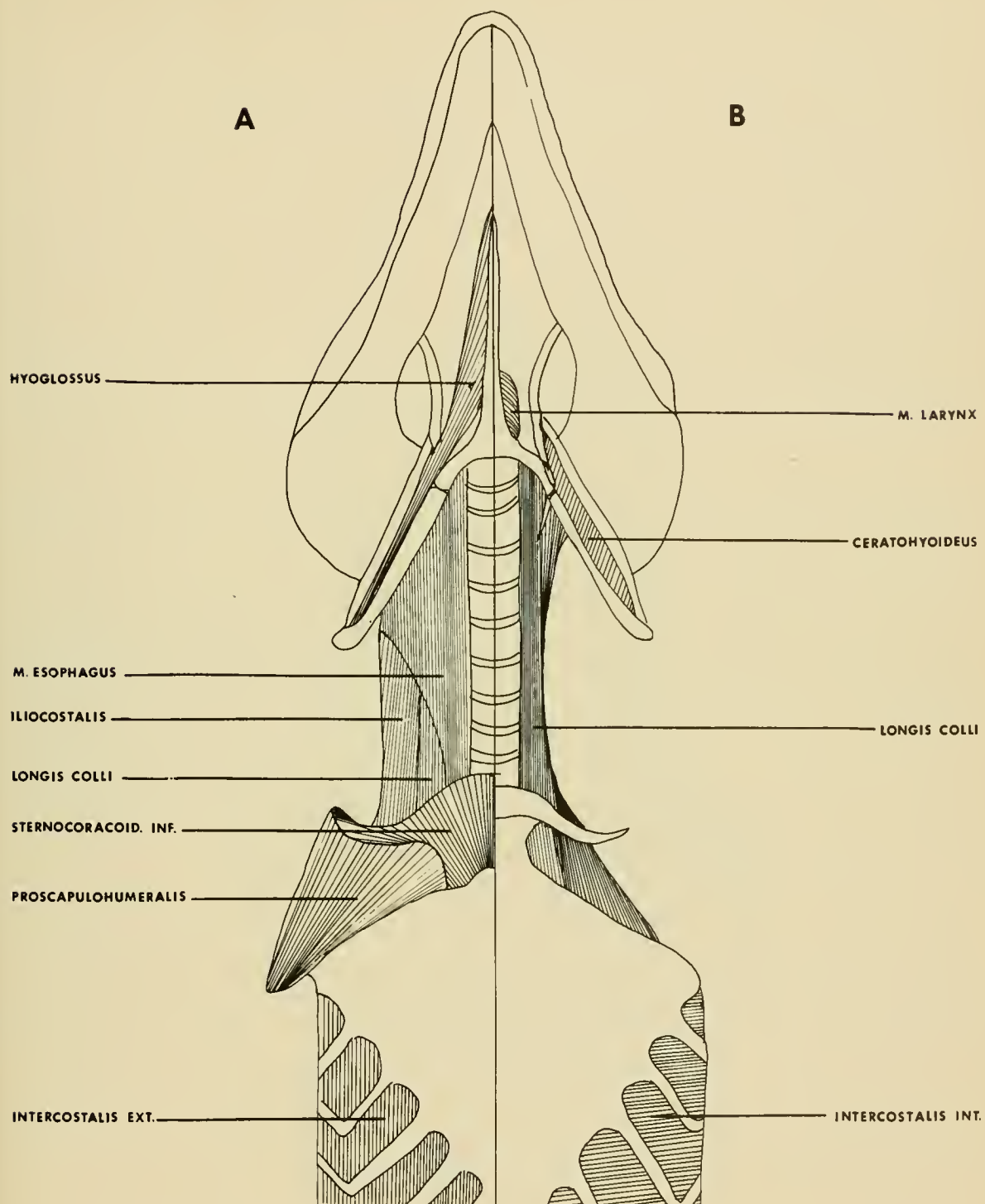
A. Superficial depth.
B. First depth.

Fig. 13. *Ameiva undulata parva*. Musculature ventral view. (2.9X)

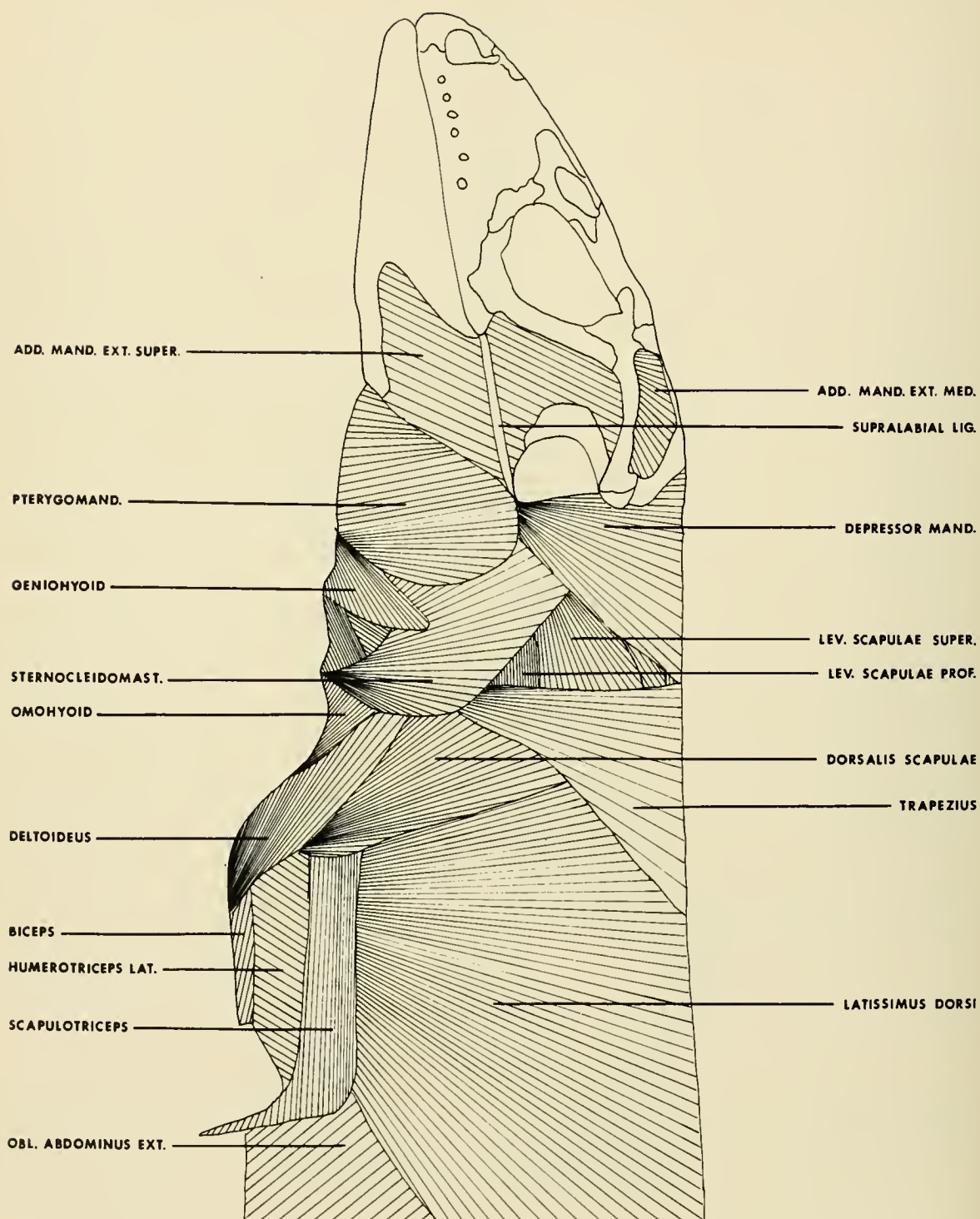


A. Second depth.
B. Third depth.

Fig. 14. *Ameiva undulata parva*. Musculature ventral view. (2.9X)

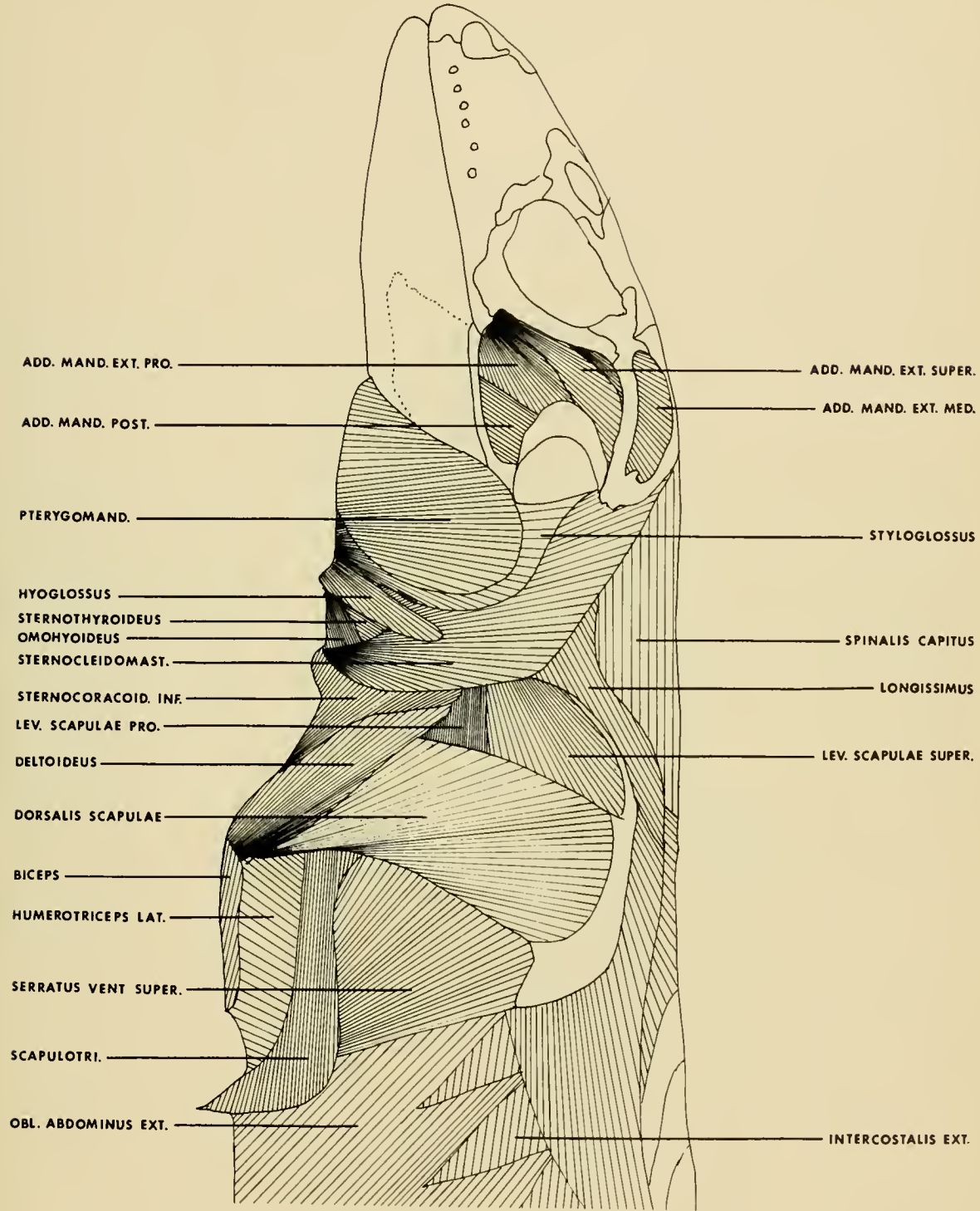


A. Fourth depth.
B. Fifth depth.



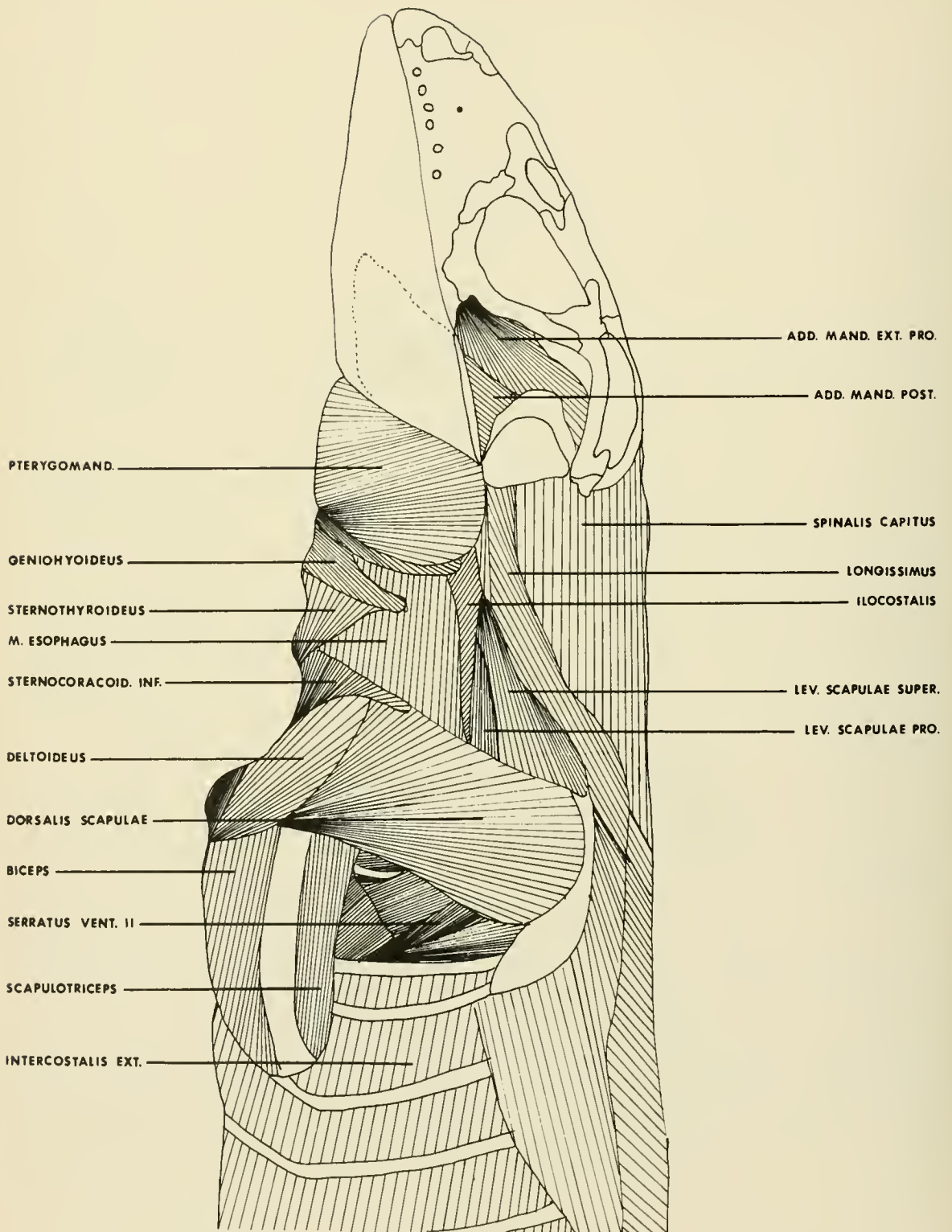
First depth.

Fig. 16. *Ameiva undulata parva*. Musculature lateral view. (2.9X)



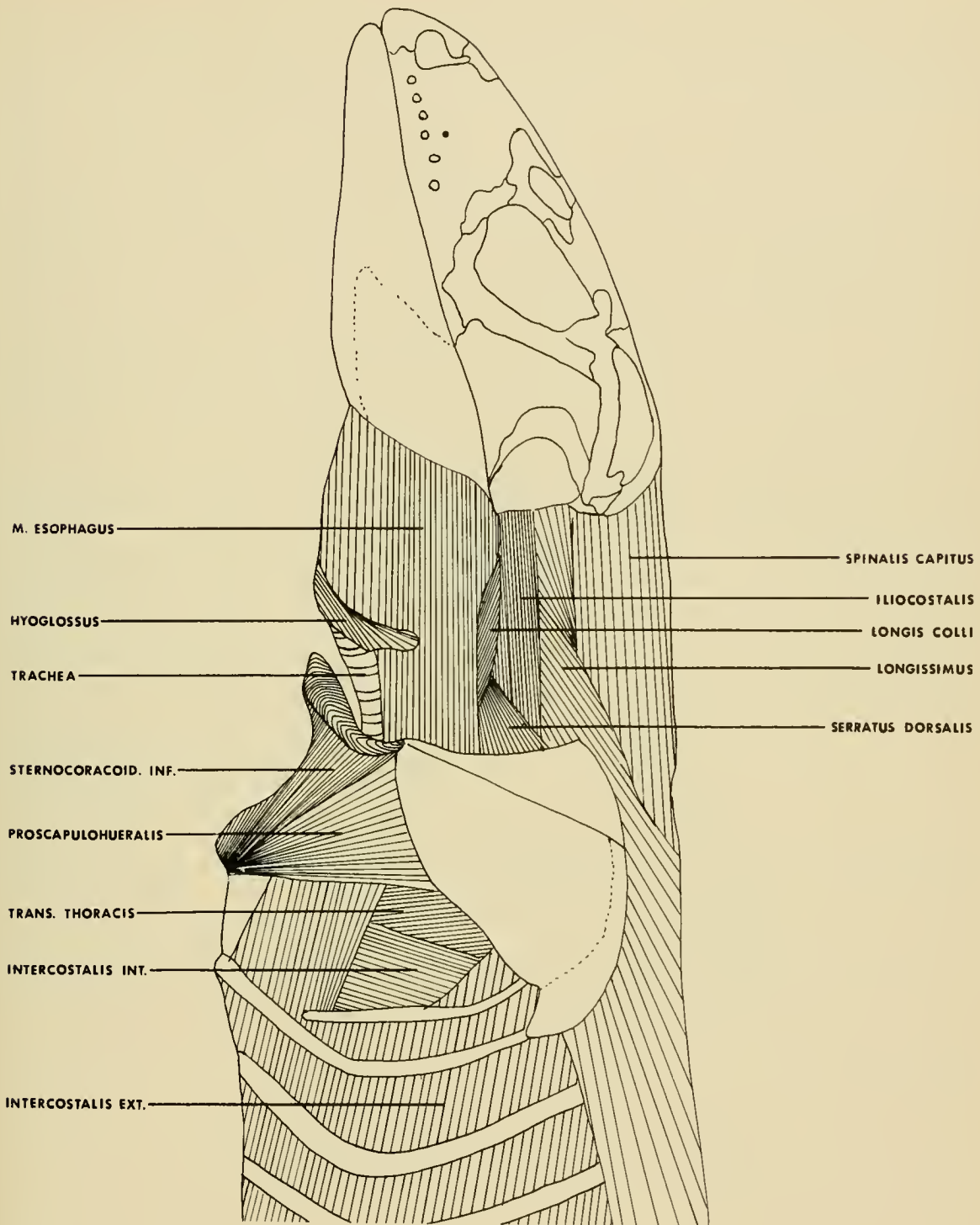
Second depth.

Fig. 17. *Ameiva undulata parva*. Musculature lateral view. (2.9X)



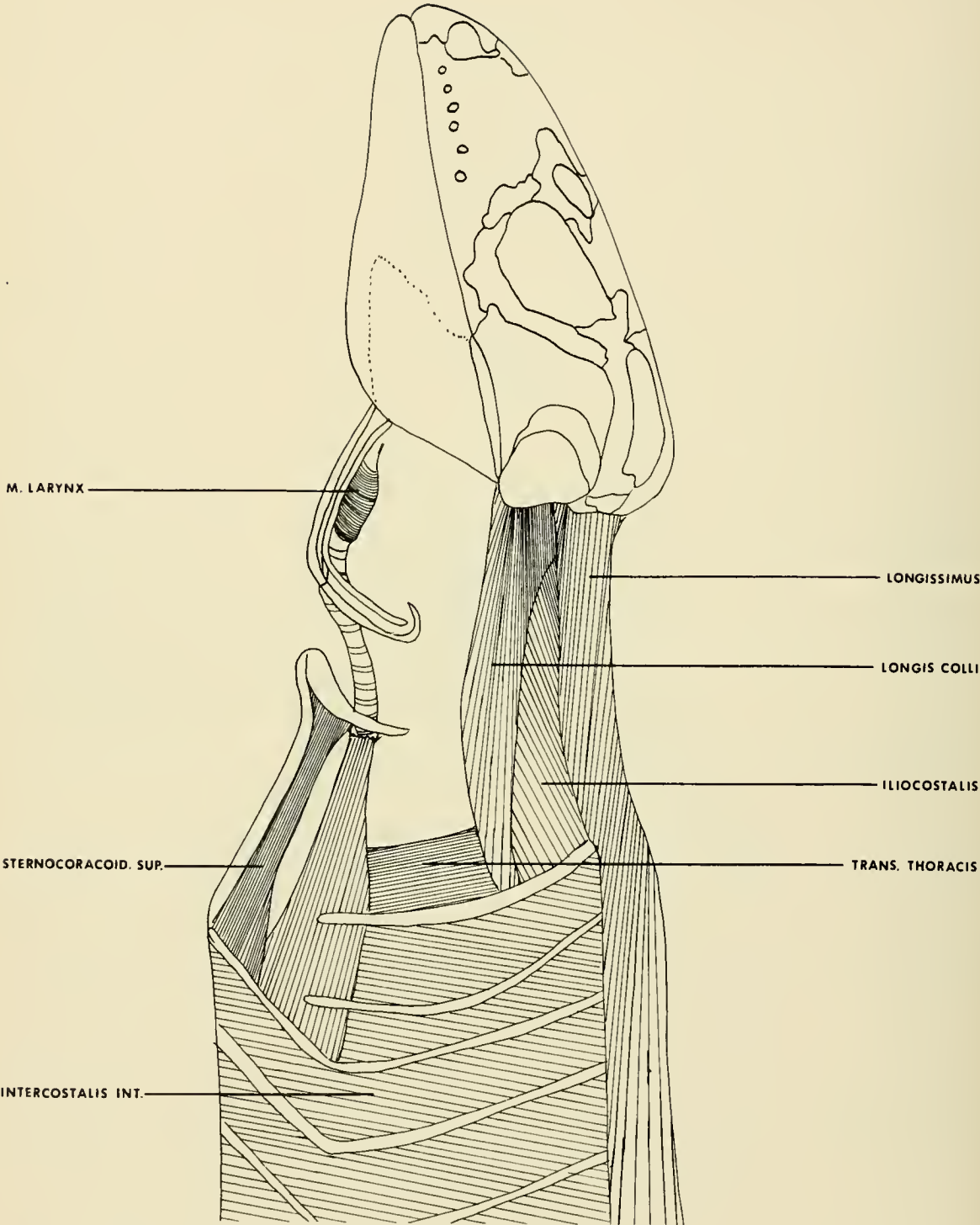
Third depth.

Fig. 18. *Ameiva undulata parva*. Musculature lateral view. (2.9X)



Fourth depth.

Fig. 19. *Ameiva undulata parva*. Musculature lateral view. (2.9X)



Fifth depth.

Fig. 20. *Ameiva undulata parva*. Musculature lateral view. (2.9X)

A. Some of the fibers of this muscle arise from the lateral and medial surfaces of an aponeurosis which extends along the medial crest of the quadrate, whereas the other fibers originate from the posterior process of the prootic. The fibers all pass antro-ventrally and insert on the dorsal surface of the articular. The body of the muscle is thin and lies lateral to the tympanic cavity and medial to the mandible and the adductor mandibularis externus.

C. Little difference is noted.

M. Biceps Brachii. (Fig. 10, 11, 13, 14, 16, 17, and 18) Howell (1936).

A. The fibers of this muscle arise near the proximal head of the humerus on the posterior edge of the scapulae, form a long, broad tendon, and pass along the ventral surface of the humerus to insert on the proximal head of the radius.

C. Little difference is noted.

M. Ceratohyoideus. (Fig. 12 and 15) Gnanamuthu (1937).

A. This is a thin muscle which proceeds between ceratobranchial 1 and ceratobranchial 2. Dorsally, it contacts the oral membrane and lies dorsal to the hyoglossus.

C. Little difference is noted.

M. Cervicomandibularis. (Fig. 10 and 13) Camp (1923).

A. The fibers of this muscle extend from the middorsal fascia to the midventral raphe proceeding posterior to the external auditory meatus and superficial to the pterygomandibularis and the majority of throat muscles. It lies just internal to the skin, and posteriorly the muscle is separated from the constrictor colli by a narrow area of aponeurosis lacking muscle fibers.

C. The division between the cervicomandibularis and the constrictor colli dorsally is less distinct with an anteroventral extension proceeding almost to the center of the dentary and covers most of the geniohyoid and some of the mylohyoideus complex.

M. Constrictor Colli. (Fig. 10 and 13) Camp (1923)

A. The muscle is the most superficial of the cervical and thorax region, arising from the superficial dorsolateral fascia of the neck and passing ventrally to insert on the extensive ventral raphe. It is internal only to the connective tissue of the skin and a few scattered fat pads. It is superficial to the depressor mandibulae and the sternocleidomastoid dorsally and ventrally it overlies the sternohyoideus, omohyoideus and a portion of the deltoideus.

C. The extent of the constrictor colli is more difficult to determine dorsally as it is somewhat fused with the cervicomandibularis.

M. Coracobrachialis. (Fig. 13 and 14) Howell (1936).

A. This is a short muscle arising from the anterior margin of the scapulae slightly dorsal to the biceps brachii and inserting mostly under cover of the deltoideus and the pectoralis on the proximal end of the humerus.

C. Little difference is noted.

M. Deltoideus. (Fig. 10, 13, 14, 16, and 17) Howell (1936).

A. The origin of the deltoideus is at the inner margin of the ventral two-thirds of the clavicle with fibers fusing at the insertion with those of the dorsalis scapulae and attaching upon the lateral portion of the proximal end of the humerus.

C. Little difference is noted.

M. Depressor Mandibulae. (Fig. 10, 16, and 18) Pöglayen-Neuwall (1954).

A. The depressor mandibulae originates on the middorsal fascia in the area of the cervical vertebrae 1-5 and inserts on the posterior end of the retro-articular process of the articular. The body of the muscle lies on the lateral surfaces of the cervical region and borders the auditory meatus anteriorly and in this area is superficial to some of the posterior fibers of the adductor mandibularis externus medius and posterior border of the tympanum. Posteriorly, it passes superficial to the anterior fibers of the trapezius and the sternocleidomastoideus. The cervicomandibularis and constrictor colli overlie most of the body of the muscle.

C. Little difference is noted.

M. Dorsalis Scapulae. (Fig. 10, 11, 16, 17, and 18) Howell (1936).

A. The dorsalis scapulae originates along an oblique line extending from a point near the dorso-caudal portion of the suprascapula to the clavicle. Origin is both from the dorsal portion of the clavicle and the dorsal margin of the girdle. The insertion is fused with that of the deltoid and attachment is upon the lateral portion of the proximal end of the humerus. The body of the muscle is deep to the trapezius and superficial to the serratus ventralis complex and the proscapulothoracalis. A part of the origin is covered by the latissimus dorsi.

C. Little difference is noted.

M. Genioglossus. (Not figured) Camp (1923).

A. This is a small muscle originating deep to the insertion of the mylohyoideus anterior on the medial surface of the dentary. It inserts into the ventral anterolateral portion of the tongue.

C. Little difference is noted.

M. Geniohyoideus. (Fig. 13, 16, and 18) Camp (1923).

A. The origin of the geniohyoideus is along the anterior margin of ceratobranchial 2 of the hyoid

apparatus and inserting in five slips along the medial surface of the dentary. The medial edge is continuous with most of the processus etoglossus which is the medial anterior projection of the hyoid apparatus (Fig. 15). The body of the muscle is superficial to the mandibulohyoideus complex, a greater portion of the ventral surface of the pterygomandibularis, the styloglossus and hyoglossus. It is deep to the mylohyoideus complex and the cervicomandibularis.

C. The insertion is by three slips with the anterior portion continuously in contact with the posterior one-third of the processus etoglossus.

M. *Humerotriceps Lateralis*. (Fig. 10, 11, 13, 14, 16, and 17) Howell (1936).

A. A muscle of the laterocentral surface of the humerus, the *humerotriceps lateralis* has its origin on the head of the humerus with fibers running distally to insert on the olecranon process of the ulna.

C. No difference is noted.

M. *Humerotriceps Medialis*. (Not figured) Howell (1936)

A. This is a muscle of the mediocentral surface of the humerus with its origin on the medial side of the humeral head and extending along the entire shaft of the humerus to insert on the olecranon process of the ulna.

C. No difference is noted.

M. *Hyoglossus*. (Fig. 11, 12, 14, 15, 17, 19) Oelrich (1956).

A. The *hyoglossus* originates on the posterior portion of ceratobranchial 2 of the hyoid apparatus and forms the body of the tongue. It is a thick broad muscle lying lateral to the ceratobranchial 2 and medial to the mandibulohyoideus III and the pterygomandibularis and is deep to the mandibulohyoideus I and II, the styloglossus and the geniohyoideus. It is superficial to the ceratohyoideus and the esophagus.

C. Little difference is noted.

M. *Iliocostalis*. (Fig. 12, 15, 18, 19, and 20) George (1948).

A. The *iliocostalis* takes a multiple origin from the ilium and fascia of the longissimus with some insertion on the anterior ribs. The anterior insertions, however, are on the atlas vertebra and the occipital region of the skull. The body of the muscle lies ventrolateral to the longissimus and dorsal to the longus colli.

C. Little difference is noted.

M. *Intercostalis Externus*. (Fig. 11, 12, 14, 15, 17, 18, and 19) Smith (1960).

A. The fibers of the *intercostalis externus* originate on the ribs and extend posteriorly to insert on the next posterior rib. It is deep to the obliquus

abdominus externus, the serratus complex and the levator scapulae complex. It is superficial to the *intercostalis internus* and *transversus thoracis*.

C. Little difference is noted.

M. *Intercostalis Internus*. (Fig. 12, 15, 19, and 20) Smith (1960).

A. The origin of the *intercostalis internus* is on the ribs with the fibers extending ventrally and slightly anteriorly to insert on the next anterior rib or the sternal portion of the same rib. It is deep to the *intercostalis externus* and superficial to the *transversus thoracis*.

C. Little difference is noted.

M. *Laryngi*. (Fig. 15 and 20) Smith (1960).

A. Muscles of the larynx are small and complex with complete dissection difficult with the technique used in this report. They are here considered as one group of muscles surrounding the laryngeal cartilages. Homologies within the vertebrates need to be determined before the individual muscles of the larynx will be of significance.

C. Little difference is noted.

M. *Latissimus dorsi*. (Fig. 10 and 16) Howell (1936).

A. The *latissimus dorsi* originates in the thoracic region of the middorsal fascia with its anterior fibers running posteroventrally and its posterior ones anteroventrally to insert near the origin of the *scapulotriceps* of the brachium onto the proximal end of the humerus. It is a sheetlike muscle which covers an extensive portion of the lateral body surface, having anterodorsal fibers deep to the trapezius while the remaining ones are deep only to the skin. It is superficial to the *serratus ventralis superficialis* and a portion of the *dorsalis scapulae*.

C. Little difference is noted.

M. *Levator Scapulae Profundus*. (Fig. 11, 14, 16, 17, and 18) Howell (1936).

A. This muscle originates from the transverse process of the atlas and inserts on the ventral one-third of the anterior border of the *suprascapulae*. It is a ventral partner to the *levator scapulae superficialis* and lies in approximately the same position with relation to the surrounding muscles.

C. Little difference is noted.

M. *Levator Scapulae Superficialis*. (Fig. 10, 11, 14, 16, 17, and 18) Howell (1936).

A. The muscle originates by means of a tendon in common with the *levator scapulae profundus* from the transverse process of the atlas and extends posterodorsally to insert on the dorsal two-thirds of the anterior border of the *suprascapula*. It is a broad, fan-shaped muscle which lies dorsal to the *levator scapulae profundus* and superficial to the axial mus-

culature and the posterodorsal fibers of the iliocostalis. The body of this muscle is deep to the constrictor colli, the trapezius and the posterior portion of the depressor mandibulae.

C. Little difference is noted.

M. Longus Colli¹. (Fig. 15, 19, and 20) Smith (1960).

A. This is the most ventral of the deep neck muscles originating on the centra of the first thoracic vertebrae and inserting on the lower portion of the centra of each of the cervicle vertebrae.

C. Little difference is noted.

M. Longissimus. (Fig. 11, 12, 17, 18, 19, and 20) George (1948).

A. The longissimus originates from the ilium, sacrum, and the neural arches; from these it proceeds anteriorly to insert on part of the neural arches of the anterior vertebrae and on part of the skull at the junction between the parietal, supraoccipital, and a small portion of the paroccipital process of the exoccipital.

C. Little difference is noted.

M. Mandibulohyoideus I. (Fig. 14) Oelrich (1956)

A. This is a slightly triangular muscle originating on the central portion of the dentary and extending two-thirds the length of the ramus to insert on the ceratohyal. It lies medial to the mandibulohyoideus II, extending deep to the cervicomandibularis and superficial to the styloglossus, hyoglossus, and mandibulohyoideus III.

C. Little difference is noted.

M. Mandibulohyoideus II. (Fig. 14) Oelrich (1956).

A. This is a short pointed muscle which originates on a posterior portion of the dentary and inserts on the anterior portion of the ceratohyal. It lies lateral to the mandibulohyoideus I and medial to the mandibulohyoideus III, running deep to the cervicomandibularis and superficial to the tongue, styloglossus and the hyoglossus. The body of the muscle is approximately the same width as the mandibulohyoideus I.

C. The muscle is much reduced in width to about one-half that of the mandibulohyoideus I.

M. Mandibulohyoideus III. (Fig. 14) Oelrich (1956).

A. This is a flat sheet of muscle originating on the posterior-most portion of the dentary and a small portion of the angular with its insertion on the ceratobranchial 1. It extends almost parallel to the mandibular ramus across the mass of the pterygomandibularis and is more or less attached to it by connective tissues. The body of the muscle is deep to the mandibulohyoideus and geniohyoideus, but is superficial to the styloglossus, hyoglossus and cerato-

hyoideus at its posterior end.

C. Little difference is noted.

M. Mylohyoideus Anterior. (Fig. 13) Camp (1923).

A. The mylohyoideus anterior is a small strip of muscle extending anterolaterally on the ventral surface of the throat, originating on the midventral raphe and inserting between the genioglossus and the geniohyoid onto the medial surface of the dentary.

C. This is the most prominent portion of the mylohyoideus and makes a definite division between the genioglossus and the geniohyoid.

M. Mylohyoideus Posterior. (Fig. 13) (Camp 1923)

A. The mylohyoideus posterior originates on the midventral raphe just posterior to the mylohyoideus anterior and immediately breaks into 9 separate divisions (4 prominent and 5 minor) which insert by interdigitation with slips of the geniohyoideus. The most posterior of the divisions is partially covered by the cervicomandibularis.

C. The muscle has only 5 divisions (3 major and 2 minor), all rather small and indistinct.

M. Obliquus Abdominis Externus. (Fig. 1, 14, 16, and 17) George (1948).

A. The origin of this muscle is by separate heads from aponeurotic tendons of the lateral and posterior surfaces of the second through eighth ribs near their dorsal articulations. The fibers then extend posteroventrally to insert along the lateral border of the abdominal musculature. The muscles of the abdominal region are highly fused to the ventral scutellation and thus difficult to detach. The body of the muscle is a thin, extensive sheet which covers most of the lateral surface of the body and is deep only to the trapezius and the latissimus dorsi.

C. Little difference is noted.

M. Omohyoideus. (Fig. 13, 14, 16, and 17) Gnana-muthu (1937).

A. This is a thick muscle of the ventrolateral surface of the neck, having its origin on the anterior border of the scapula and then proceeding anteroventrally to insert on the proximal end of the basihyal and along ceratobranchial 2. It is deep to the posterior portion of the cervicomandibularis and the anterior portion of the constrictor colli, superficial to the anterior portion of the sternothyroideus and a small portion of the esophagus, and lies lateral to the sternohyoideus.

C. The muscle is much broader, covering the sternohyoideus to an area midway between the hyoid apparatus and the sternum.

M. Pectoralis. (Fig. 13) Camp (1923).

A. The pectoralis is an extensive superficial muscle of the sternal region, originating from the inner

angle of the clavicle, the interclavicle, the sternum and the midventral raphe and inserting on the proximal end of the humerus. It is superficial to the sternum, some of the sternal ribs and the coracoid and is deep only to the skin of the chest region.

C. Little difference is noted.

M. Proscapulothoracalis. (Fig. 12, 15, and 19) Howell (1936).

A. The proscapulothoracalis originates on the anteroventral margin of the scapula with fibers proceeding ventrally which immediately join those of the coracothoracalis of the same layer. Toward the insertion, the latter muscle passes over a small ligament while the former passes beneath it to insert upon the humerus between the medial and lateral heads of the humerotriceps. It lies superficial to the sternocoracoides superior and deep to the deltoideus.

C. Little difference is noted.

M. Pterygomandibularis. (Fig. 10, 11, 13, 14, 16, 17 and 18) Oelrich (1956).

A. This is the largest muscle of the lateral surface of the skull, originating on the pterygoid along the margin of the infraorbital foramen by means of a large tendon attached to the ectopterygoid process. The fibers extend posteriorly and posterodorsally to cover the ventral and lateral surfaces of the angular and surangular they then continue posteriorly along the condyle of the quadrate and insert on the angular process of the articular. It is deep to the cervicomandibularis dorsally and the mandibulohyoideus III ventrally and lies superficial to the esophagus.

C. The muscle is not as bulky, but otherwise little difference is noted.

M. Scapulotriceps. (Fig. 11, 13, 14, 16, 17, and 18) Howell (1936).

A. The origin of the scapulotriceps is on the scapula near the glenoid fossa. The fibers then loop around the insertion of the latissimus dorsi and proceed distally to insert on the olecranon process of the ulna.

C. Little difference is noted.

M. Serratus Dorsalis. (Fig. 11, 12, 18, and 19) Howell (1936).

A. This muscle consists of three ribbonlike slips of muscle which partially overlap one another in such a way that they appear serratuslike from a dorsal view when the suprascapula is pried away from the lizard's body (as in Fig. 11B). It arises by fasciculae from the lateral surfaces of the three cervical ribs and then passes slightly dorsolaterally to insert separately, but slightly overlapping one another, along the medial surface of the suprascapula near its dorsal border. Although the muscle is partially continuous with the serratus ventralis complex, it lies medial and some-

what dorsal to the ventral slips.

C. Little difference is noted.

M. Serratus Ventralis I. (Fig. 11) Howell (1936).

A. The serratus ventralis I originates centrally slightly beneath the serratus dorsalis on the first two ribs and inserts on the anteromedial border of the scapula. The body of the muscle is deep to the subscapularis and superficial to the intercostalis externus.

C. Little difference is noted.

M. Serratus Ventralis II. (Fig. 11 and 18) Howell (1936).

A. This muscle originates immediately ventral to the last slip of the serratus dorsalis and its origin is centrally on the posteromedial portion of the scapula and is immediately ventrolateral to the serratus ventralis I.

C. Little difference is noted.

M. Serratus Ventralis Superficialis. (Fig. 10, 14, and 17) Howell (1936).

A. The muscle originates by means of several slips from the first two ribs, then proceeds anterodorsally to insert on the posterior border of the scapula. The body of the muscle is deep to the latissimus dorsi and superficial to serratus ventralis I and II as well as intercostalis externus.

C. Little difference is noted.

M. Spinalis Capitus. (Fig. 11, 12, 17, 18, and 19) George (1948).

A. This is the large anterior epaxial muscle originating in common with the spinalis cervicis and inserting on the posterior margin of the parietal. It is deep only to the middorsal fascia and the dorsal portion of the cervicomandibularis and is superficial to the longissimus, iliocostalis and longus colli.

C. Little difference is noted.

M. Sternocleidomastoideus. (Fig. 11, 13, 14, 16, and 17) Howell (1936).

A. Sometimes called the episternocleidomastoid (Robison and Tanner, 1962), it is a thick, ribbonlike muscle obliquely crossing the lateral surface of the cervical region, originating by a superficial aponeurosis from the posterior cranial region along the extreme posterolateral margin of the parietal and the parietal process and inserting along the dorsal margin of the clavicle with a small slip attaching to the anterior portion of the sternum. Anterodorsally, it is deep to the depressor mandibularis; otherwise, it lies superficial to the sternothyroideus, levator scapulae profundus and superficialis, and the deep epaxial musculature.

C. Little difference is noted.

M. Sternocoracoideus Inferior. (Fig. 11, 12, 14, 15, 17, 18, and 19) Howell (1936).

A. This is a somewhat confusing muscle which arises from the ventral surface of the sternum and proceeds anteriorly over the end of the clavicle and inserts on the ventral coracoid end of the scapula thus covering the clavicle almost entirely.

C. Little difference is noted.

M. Sternocoracoideus Superior. (Fig. 15 and 20) Howell (1936).

A. The sternocoracoideus superior is an internal sternal muscle originating from most of the dorsal surface of the sternum and inserting by a broad thin tendon on the ventral portion of the scapula, appearing to insert on the clavicle.

C. Little difference is noted.

M. Sternohyoideus. (Fig. 13 and 14) Camp (1923).

A. The sternohyoideus is a relatively broad, flat muscle of the ventral surface of the neck region. It originates on the sternum and inserts on portions of the basihyal and anterior section of ceratobranchial 2. It lies medial to the omohyoideus anteriorly and the sternocleidomastoideus posteriorly. It is deep to the posterior portion of the cervicomandibularis and anterior portion of the constructor colli and lies superficial to the esophagus.

C. Little difference is noted.

M. Sternothyroideus. (Fig. 14, 17, and 18) Camp (1923).

A. This is a large flat muscle extending along the ventrolateral side of the neck, originating in a sheet from the anterior portion of the sternum and inserting along most of the posterior length of ceratobranchial 2. The body of the muscle lies deep to the sternocleidomastoideus and the posterior portion of the omohyoideus. It is superficial to the esophagus.

C. Little difference is noted.

M. Styloglossus. (Fig. 11, 13, 14, and 17) Smith (1960).

A. Although the exact extent of this muscle is somewhat questionable because of the fascia on its posterodorsal surface, it appears to originate by means of a thin sheet of fascia from the posterior region of the cranium and quadrate and inserts on the mandibular symphysis of the dentaries. It covers the hyoglossus and forms a small part of the basal sheath which covers the posterior margin of the tongue.

C. The origin appears almost tendinous posterodorsally and anteroventrally no basal sheath is contributed to the tongue.

M. Subscapularis. (Not figured) Howell (1936).

A. The subscapularis arises from the base of the medial side of the suprascapula and the adjoining portion of the scapula; its fibers converge to a tendinous insertion upon the retractor process of the humerus. It is deep only to the scapula, but is superficial to the serratus ventralis complex as well as a portion of the serratus dorsalis.

C. Little difference is noted.

Supralabial Ligament. (Fig. 16) New Name.

A. This is a strong superficial ligament of the lateral surface extending beneath the supralabial scales of the skin from the rostral area to insert on the anteroventral margin of the quadrate. It is deep only to the fascia of the skin and is superficial to the pterygomandibularis.

C. Little difference is noted.

M. Transversus Thoracis. (Fig. 19 and 20) Smith (1960)

A. In contact with the peritoneal membrane internally, the transversus thoracis arises by means of fascia from the pelvis to the neck region and lies, for the most part, between the second thoracic vertebra and the humerus. Its fibers extend almost vertically and insert on the inner surfaces of the thoracic ribs, the lateral border of the sternum, and the dorsal surface of the abdominal musculature. It is deep to all of the thoracic musculature.

C. Little difference is noted.

M. Trapezius (Fig. 10 and 16) Howell (1936).

A. This is an extensive, superficial muscle located on the dorsolateral surface of the cervical and thoracic regions. It is the most superficial muscle of the area with the exception of the depressor mandibularis and the constrictor colli which originate on the mid-dorsal raphe in the area of the lower cervicals and insert on the crest of the anterior margin of the suprascapula, the superficial fascia along the clavicle and the anterior margin of the pectoralis to the origin of the sternocleidomastoideus. This muscle varies greatly in thickness throughout its extent. Posteriorly, it is considerably developed, this being the major part to insert on the suprascapula. However, anteriorly, it comes to be only one muscle layer in thickness. The body of the muscle is superficial to the levator scapulae superficialis and profundus as well as the dorsal portion of the dorsalis scapulae.

C. Little difference is noted.

DISCUSSION

Phylogenetic speculations on reptiles have been based upon information derived from three areas: (1) the fossil record, (2) the geographic distribution, and (3) the comparative morphology of living genera (Camp, 1923). The third area has been the main focus of attention in this report. The most reliable hypotheses of phylogeny require careful examination of all potential data; therefore definitive phylogenetic conclusions are not justified by this study. Howes (1902) discussed the idea that comparative morphology is the primary practical basis of a working classification. He further noted that comparisons should be first made on closely related forms, passing later to larger and less closely related groups. The present comparisons, restricted to *Cnemidophorus* and *Ameiva* provide an initial step. The genus *Cnemidophorus* is a probable offshoot of *Ameiva* as speculated by Barbour and Noble (1915) and as well by Burt (1931b).

Camp (1923) listed 34 different paleotelic characters of importance in considerations of phylogeny as determined by comparative morphology. Although some of these characters are of little significance below the family level, those which are of importance to phylogeny of the genera discussed in this report include in the order of significance listed by Camp: (1) fusion of median skull elements, (2) the postorbital-postfrontal, (3) the lacrymal, (4) mandibular teeth, (5) palatine teeth, (6) throat musculature, (7) the lower jaw, (8) the os intermedium (9) the epipterygoid, and (10) the shoulder musculature. These are not all of the phylogenetically significant characters which have been discussed in such texts as those by Smith (1960) and Romer (1964), but the list may lend an index to phylogenetic studies.

In the following discussion, osteological variables are treated first, then myological variables. The two sets of variables together should provide a more reliable bases for speculation on phylogenetic relationships than one of them alone. As pointed out by Nopcsa (1928), osteological characters alone are insufficient to distinguish all of the Teiidae from all of the Iguanidae, for example, and it is probable that the reverse is also true.

Osteology.

Elements of the skull and lower jaw (as indicated in fig. 1-8) show considerable variation between the members of the two genera described. Considerable variation is noted in the general appearance of the skull and lower jaw. In *A. u. parva*, the skull can be considered heavily ossified with a rugose dorsal surface; deep indications of indentation for integumentary scutellation are evident and an os palpebrae is evident in the anteromedial border of the

orbit. In the lower jaw, there is a slight lateral torsion of each ramus, the articular and angular are at almost right angles to each other, and the ventral surface of the dentary is rugose. In *C. t. septentrionalis*, the skull is comparatively lighter with a relatively glabrous dorsal surface. There is little indication of indentation of integumentary scutellation and the anteromedial border of the orbit is cartilaginous. In the lower jaw, there is no lateral torsion, the articular and angular essentially form a straight line, and the ventral surface of the dentary is relatively glabrous.

For further references to variation of the separate elements is noted in the general description. Elements discussed in which a difference is noted include the basioccipital, ectopterygoid, exoccipital, frontal, jugal, lacrimal, maxilla, nasal, os palpebrae, palatine, parietal, postorbital-postfrontal, prefrontal, premaxilla, prootic, pterygoid, quadrate, supraoccipital, and most of the elements of the lower jaw except the splenial.

The most unstable element of osteological import appears to be the intermedium of the wrist. Romer (1956) points out that fusion and sometimes complete loss of some wrist bones is common in lizards. With the methods used in this report, an element as minute as the intermedium is difficult to locate on small specimens and may account for its apparent absence in some of the species and subspecies observed. Possession of this element may indicate primitiveness, but this is questionable because of its variation even between subspecies. The degree of ossification of this structure and other carpals is probably a function of age of the individual. It is recognized that a need for using larger series in most of the species is necessary for a complete study; however, the data presented seems significant since all of the *Ameiva undulata* group examined appear to possess the element whereas it is seemingly absent in examples of the *Cnemidophorus tigris* group examined by us.

Teeth.

The teeth of *A. u. parva* and *C. t. septentrionalis* show some similarity of shape and relative size, but they differ considerably in the positioning and number of cusps on specific teeth. Perhaps the greatest difference noted was the absence of pterygoid teeth in *A. u. parva*. Camp (1923) suggests that the presence of these teeth may be of paleotelic significance, but he hastened to add that the absence of such teeth may or may not be of significance owing to the likelihood of dropping out or the migration and development of cutaneous tooth buds from one bone to another in the course of recent phylogeny.

Age is also exhibited by tooth structure of both genera as the older specimens have some of the posterior accessory cusps well worn or reduced to small swellings. Several of the teeth are also loose or missing (replacement) and broken.

Myology.

The problems of myological research are at times rather complex. Huntington (1903), Camp (1923), Romer (1956) and Smith (1960) indicate that the musculature of major groups such as orders and classes is rather plastic and variable and are, thus, rather difficult to interpret. At the family level, however, myology appears to be a sufficiently stable character to be of phylogenetic use. Tanner (1952) indicated that in Mexican and Central American groups of the salamander family Plethodontidae the musculature is consistent enough to define genera. This conclusion has been further supported by Wake (1966) on the osteology of the plethodontid salamanders and by work in reptilian myology by Robison and Tanner (1962), and Avery and Tanner (1964). The two genera of the family Teiidae examined in this report seem to support this conclusion. Of the forty-nine muscles dissected in *A. u. parva* and compared in *C. t. septentrionalis*, only six differed significantly between the two genera as far as configuration, origin, insertion, or size was concerned. Because of the relative stability of the myology within these two

genera, this could perhaps be used as a tool for interpretation of phylogenies and variations.

The greatest myological variation appears to be centered around the anterior segments of the ventral musculature. In *A. u. parva*, the mylohyoideus complex interdigitates frequently with the geniohyoideus by nine separate bundles, whereas in *C. t. septentrionalis* this complex interdigitates in only five bundles of rather simple structure. Camp (1923) seems to believe that the variation in this musculature is a good indicator of primitiveness. He pointed out that above the family level a primitive saurian condition is represented by eight or more interdigitation bundles of these two muscle groups.

Other myological variations for *A. u. parva* include a distinct division of the cervicomandibularis by the constrictor colli, a mandibulohyoideus II which is the same width as the mandibulohyoideus I, and an omohyoideus which is rather narrow and located ventrolaterally in the neck region. In *C. t. septentrionalis*, there is a dorsal fusion of the cervicomandibularis with the constrictor colli, the mandibulohyoideus II is only one-half the width of the mandibulohyoideus I, and the omohyoideus is relatively broad, extending ventrally to the midcentral region of the neck.

The differences in configuration of these muscles may indicate that the variability is not suited for phylogenetic comparisons between these two genera, or they may support the distinction of the two genera. Further study of the entire family would be necessary before definitive conclusions could be reached.

CONCLUSIONS AND SUMMARY

The anterior osteological elements of the skull, lower jaw, and wrist along with the anterior myological characters discussed and figured in this report suggest that *A. u. parva* and *C. t. septentrionalis* are members of distinct groups which can be differentiated by internal morphologic characters. Although comparisons were restricted to highly geographically separated individuals of the same family, their general body form and structure appear to be similar.

A great number of anatomical structures are shared in common, but the significant differences between them include:

1. General skull appearance.

The skull of *C.* is generally lighter, that is the bones are thinner, than in *A.* and with a larger portion relatively glabrous on the dorsal surface with little indication of integumentary scutellation. The most notable differences are found in the occipital region of *A.* where much

fusion of elements and exact suturing is difficult to distinguish. In *C.*, the occipital elements are easily distinguished.

2. Skull elements.

Those elements of greatest difference and significance are noted in the sections titled descriptions and discussion. The elements include the ectopterygoid, exoccipital, frontal, jugal, os palpebrae, postorbital-postfrontal, premaxilla, and the quadrate.

3. Lower jaw elements.

Those elements of greatest difference and significance are noted in the sections titled descriptions and discussion. The elements include the angular, articular, and dentary.

4. Foramina of the skull and lower jaw.

The foramina of significant difference

between the two genera are noted in the sections titled description and discussion. These include the infratemporal fenestra, mental foramina, nasal foramina, palatine canals, splenial foramina, surangular foramina, and the supra-labial foramina.

5. The teeth of the maxilla, dentary, and pterygoid.

The teeth are mostly peglike with the first accessory cusp of the dentary appearing on tooth 5 in *C.* and tooth 6 in *A.* There are eight peglike teeth on the premaxilla of *C.* and ten on the premaxilla of *A.* The greater number is a probable indicator of greater antiquity. In the maxilla a posterior accessory cusp is found on the second tooth of *A.* and the sixteenth of *C.* Perhaps the most significant point is that five peglike teeth occur on the pterygoid of *C.* and none were found on *A.*

6. The intermedium wrist element.

An intermedium was found to be present in the manus of *C. communis*, *C. gularis*, *C. burti*, *C. sexlineatus*, *A. u. parva*, *A. u. hartwegi*, and *A. u. sinistra*. It is either absent or questionably present in *C. t. tigris*, *C. t. septentrionalis*, *C. t. gracilis*, *C. t. canus*, *C. t. aethiops*, *C. gularis*, *C. exsanguis*, *C. d. deppei*, *C. d. lineatissimus*, *C. h. hyperythrus*, *C. o. lemniscatus*, and *A. auberi*. It is evident from the above distribution that the presence or absence of the intermedium may not be of paleontologic significance at the generic level, but may be at the specific level. It may also be intraspecifically variable.

7. The musculature.

The greatest myological variation appears to be centered around the anterior segment of the ventral musculature. The mylohyoideus com-

plex interdigitates frequently with the geniohyoideus in *A. u. parva*. Nine separate bundles were found in the species studied. Camp (1923) stated that above the family level in suarians, eight or more bundles was a valid indicator of primitiveness. The other muscles of generic variation include the m. cervicomandibularis, m. constructor colli, m. mandibulohyoideus II, m. omphyoideus, m. styloglossus and the associated basal tongue sheath.

The anatomical differences existing in the sheath associated with the tongue of *A. u. parva* is of special significance. A basal sheath is connected to the tongue sheath and extends for attachment to cranial and mandibular bones. This establishes a real anatomical basis for the tongue sheath character now used by some to separate these genera. Further exploration of species in these genera should be made to determine the stability of the character. This is particularly true in view of the comments made by Burt (1931b) concerning this structure, which, based on his findings, may be an inadequate character to separate these genera.

It is evident from the findings that specialization has occurred not only intergenerically but intragenerically, and care must be taken to distinguish the two levels of variation. Clearly the presence or absence of the intermedium is of little significance intergenerically, but may be of importance intragenerically. The presence or absence of the pterygoid teeth may also fit this category, but with our present understanding of its paleontologic significance within this family it is impractical to draw a conclusion. Barbour and Noble (1915) and Burt (1931b) concluded from their study of external morphology that *Ameiva* is a more primitive genus than *Chemid phorus*. Our observations of osteological and myological structures which are seemingly of paleontologic significance also support this conclusion.

¹It is to be noted that the terminology of this muscle has not been determined in the literature. The name of a similarly placed mammalian muscle is temporarily adopted until complete homologies can be determined.

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**PINYON-JUNIPER SUCCESSION
AFTER NATURAL FIRES ON RESIDUAL SOILS OF
MESA VERDE, COLORADO**

by

James A. Erdman



BIOLOGICAL SERIES—VOLUME XI, NUMBER 2

JUNE 1970

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Frontispiece. The Morfield Burn of 1959 several days after the natural fire was suppressed. Ash and mud were temporarily impounded behind this road across East Canyon.

**Brigham Young University
Science Bulletin**

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PINYON-JUNIPER SUCCESSION AFTER NATURAL FIRES ON RESIDUAL SOILS OF MESA VERDE, COLORADO

by

James A. Erdman*

ABSTRACT

A mountain brush vegetation typified by Gambel oak (*Quercus gambelii*) and serviceberry (*Amelanchier utahensis*) dominates the uplands of Mesa Verde National Park. There is evidence that this brush element is a successional stage that has been maintained by repeated natural fires in a large part of the Mesa Verde landscape. This study was conducted to determine the role of fire in the region's ecology, the nature of the climax pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) vegetation, and the major successional stages that lead to the climax condition.

Three postburn plant communities and two climax stands overlying residual soils at elevations of about 7,500 feet were studied. The successional stands had been burned through natural causes in 1873, 1934, and 1959. The earliest date was determined by cross-dating trees affected by the fire with the Mesa Verde master chronology, since the fire antedated any written records of the region. Pith dates from pinyon pines in the climax forest stands indicated an age of about four centuries.

Permanent sample plots representative of each stand were established, and the vegetation was analyzed using a modification of the line intercept and macroplot methods. The vascular species that occurred in each sample were noted, and their cover value and frequency were summarized.

Plant succession proceeds rapidly from a pioneer stage of the shade and competition intolerant weeds,

Helianthus annuus and *Chenopodium pratericola*, to a meadow stage dominated by the native grasses, *Oryzopsis hymenoides*, *Sitanion hystrix*, and *Poa fendleriana*. In the most recent burn, several species of perennial exotic grasses have been introduced to check erosion.

After about 25 years, a crown-sprouting brush element, consisting primarily of *Quercus gambelii*, *Amelanchier utahensis*, *Cercocarpus montanus*, and *Purshia tridentata* becomes the dominant vegetation. At this time, seedlings of *Pinus edulis* and *Juniperus osteosperma* are also established. This open shrub stage gradually becomes more dense, and in about 100 years forms a thicket stage. Young trees come up through the shrubs, eventually overtopping them. As the fire sere proceeds toward a climax condition, the brush species are gradually suppressed by the maturing forest. After several centuries, the understory is composed mainly of a sparse shrub component, a grass (*Poa fendleriana*), prickly-pear (*Opuntia polyacantha*), and several forbs.

The data tend to support the theory that recurrent fires throughout previous centuries have permitted a chaparral-like, floristically rich shrub vegetation to persist as a fire climax along the uplands of Mesa Verde National Park. Under the present management policies of fire suppression, however, a pinyon-juniper forest is slowly replacing the former extensive shrub vegetation.

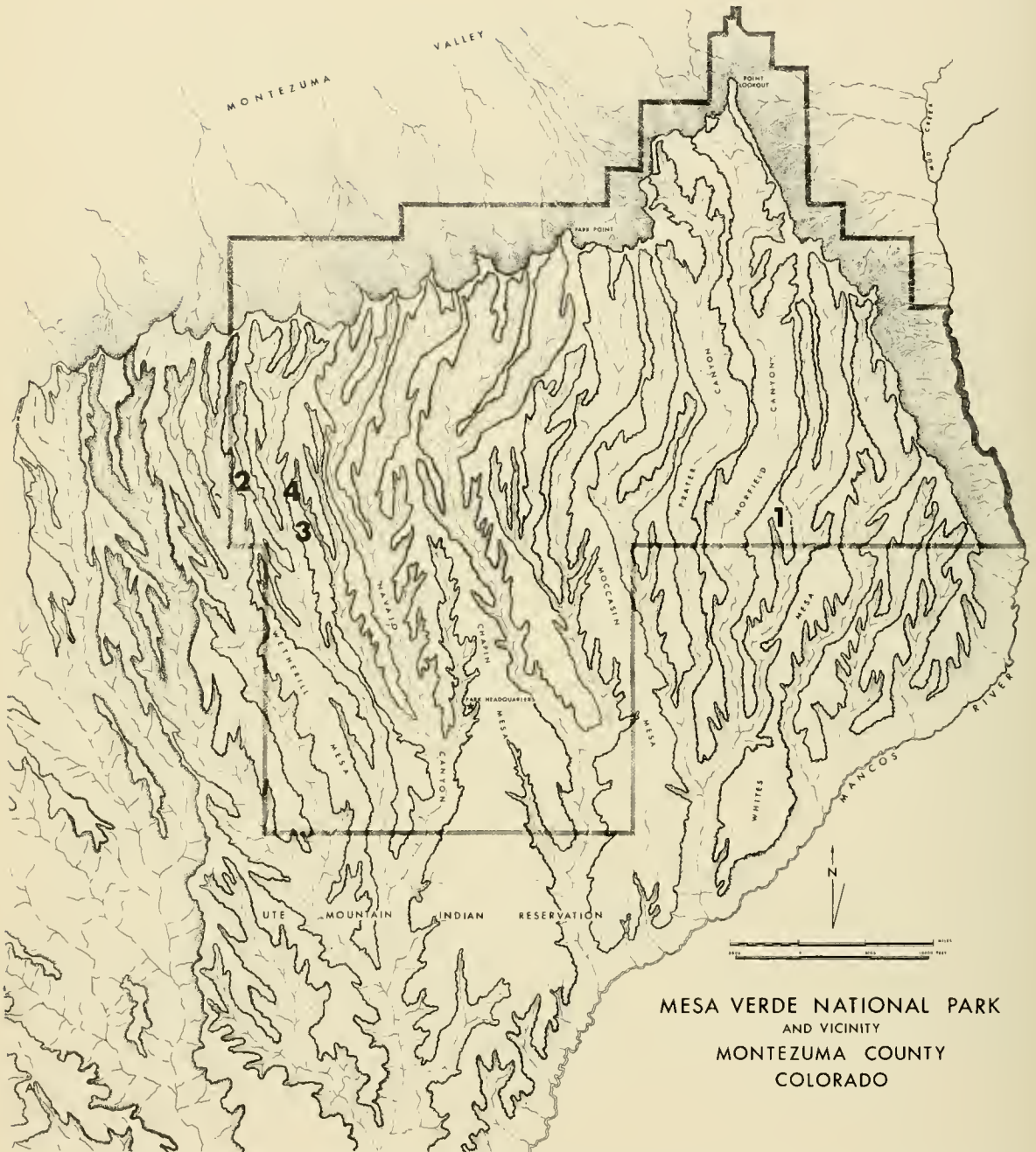
INTRODUCTION

Mesa Verde, a highly eroded plateau in southwestern Colorado (Fig. 1), is on the eastern edge of the Colorado Plateau physiographic province. A pinyon-juniper forest dominates most of the mesa, but dense brush vegetation is common at higher elevations, especially within the boundaries of Mesa Verde National Park. The ecological status of the brush has been a puzzle because, while it appears relatively stable, other sites on the mesa with an apparently similar environment are occupied by stands of pinyon-juniper. Moreover, evidences of fire predating the recent human occupation of the area suggest that

the brush may be a product of fire (Anderson, 1961).

As a member of the staff of the park's Wetherill Mesa Project (Osborne, 1964), I was charged with helping to determine the environmental conditions that existed during the prehistoric Indian occupation of the area, which extended up to the close of the thirteenth century. It was apparent that an understanding of succession following fires would be helpful in the paleoenvironment researches. A fire in Morfield Canyon, in July 1959, provided me with an opportunity to study early stages in the sere, and shortly thereafter I began an intensive investigation of

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MESA VERDE NATIONAL PARK
AND VICINITY
MONTEZUMA COUNTY
COLORADO

Fig. 1. Map of the eastern part of Mesa Verde. Residual soils cover the upper third of the mesa, at elevations generally above 7,500 feet. The study sites are as follows: 1) Morfield Burn, 2) Wetherill Burn, 3) Long Mesa Burn, and 4) the Long Mesa Climax. An additional climax site that was studied is located on the Ute Mountain Indian Reservation about 2 miles west of the Wetherill Burn.

the mountain brush, or chaparral (Bader, MS.; Anderson, 1961).

The Mesa Verde sandstones and shales of Upper Cretaceous age (Wanek, 1959) rise 1,500 feet above the valleys to the north which reach a maximum elevation of 8,500 feet. These beds dip southward towards the Mancos River. Here the canyons attain depths of 1,000 feet. Travel across the mesa, therefore, is generally along the upper reaches, where the relief consists of rolling swales and ridges.

Residual soils are developed from the underlying sandstone on the narrow, more easily eroded ridges of the higher parts of Mesa Verde—the area under consideration. Most of the soils on the remainder of the plateau, however, appear to be eolian in origin (Arrhenius and Bonatti, 1965), with accumulation continuing even today though at a minimal rate. The calcium carbonate content is highly variable; in some places it forms a thick caliche layer, while in others free lime is absent.

The climate of Mesa Verde is mild, for in this semi-arid region fair weather prevails throughout the year.

Temperatures on the mesa (Table1) are suprisingly moderate, considering the altitude. This is a result of both generally continuous winds from the southwest and lack of cold-air drainage. Extreme temperature fluctuations, rare on the mesa tops, are pronounced along the canyon floors, however (Erdman, Douglas, and Marr, 1969).

TABLE 1
SUMMARY OF MESA VERDE CLIMATE,
U.S. WEATHER BUREAU STATION
AT HEADQUARTERS, CHAPIN MESA.
ELEVATION 7,070 FEET.
RECORD PERIOD, 1923-1963*

Month	Air Temperature, °F			Precipitation in inches
	Maximum	Minimum	Mean	
January	62	-20	29.8	1.93
February	68	-15	33.0	1.95
March	72	4	38.6	1.76
April	84	9	48.1	1.32
May	90	23	57.0	1.05
June	101	32	67.4	.70
July	102	43	72.9	1.68
August	101	41	70.8	2.01
September	94	28	64.4	1.53
October	85	13	52.7	1.66
November	75	-3	39.5	.98
December	67	-6	32.1	1.71
Annual	102	-20	50.5	18.28

*U.S. Weather Bureau, 1964, and Mesa Verde National Park weather records.

Precipitation is irregular. A proportionately large amount comes as snow during the late winter months. Normal snowfall is 78 inches. The typically dry months of May and June are followed by a period of intense and often highly localized thunderstorms. Rainfall during the late summer and early autumn may be heavy, but because of rapid runoff and high evaporation it is much less effective than winter moisture in recharging ground water supplies. Except for the Mancos River, which skirts the mesa on the south, the only natural water supplies available to wildlife are occasional springs, seeps, and potholes that have been filled by rains or melted snow.

Pollen studies by Martin and Byers (1965) and simultaneous dendroclimatic investigations by Fritts, Smith, and Stokes (1965) indicate that the climate has been relatively stable in the Mesa Verde region during the past millennium. This period would seem to be adequate for plant species adapted to the climatic conditions here to establish themselves and achieve stable communities.

Mesa Verde lies within the pinyon-juniper climax region, an area of 60 million acres lying mostly in Nevada, Utah, Colorado, Arizona, New Mexico, and western Texas (Arnold, Jameson, and Reid, 1964). These forests have been described by Howell (1941), Woodbury (1947), Merkle (1952), and Woodin and Lindsey (1954).

I have not used Merriam's terms, Upper Sonoran and Transition zones, since I agree with Johnsen (1964) that "The terms Upper and Lower Sonoran are occasionally used in generalized, limited area studies by nonbotanists to avoid detailed descriptions of flora and fauna; and, as such, the terms have a general but limited descriptive value."

Most of the plateau is mantled with stands of pinyon pine (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* (Torr.) Little). The areas underlain by loess have an understory dominated by muttongrass (*Poa fendleriana* (Steud.) Vasey), and those underlain by residual soils have an understory dominated by shrubs. *Dominance*, as used here, is based upon "an approximation of the area over which a plant exerts its influence upon other components of the ecosystem" (Daubenmire, 1959).

Elements of the montane flora are common at the more mesic sites in the Mesa Verde area. These sites are dominated by aspen (*Populus tremuloides* Michx.), ponderosa pine (*Pinus ponderosa* Dougl.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), or a combination of all three. As an extension of the Great Basin flora to the west, big sagebrush (*Artemisia tridentata* Nutt.) assumes a climax status on the deep, friable, alluvial terraces in the canyons.

The flora of Mesa Verde is characterized by Madro-Tertiary species (Weber, 1965). In addition to the pinyon-juniper element, the mountain-brush thickets so extensive along the North Rim contain several species belonging to this assemblage, the principal one of which is Gambel oak (*Quercus gambelii* Nutt.). Some of the Madro-Tertiary representatives, however, are exceedingly rare relicts in the Mesa Verde. Among these are single-leaf ash (*Fraxinus anomala* Torr. ex S. Wats.), big-toothed maple (*Acer grandidentatum* Nutt. ex T. & G.), and Ajo oak (*Quercus ajoensis* Muller), a recent addition to the Colorado flora (Erdman, Weber, and Tucker, 1962).

This study is concerned with the mountain-brush element associated with the pinyon-juniper forest on residual soils.

METHODS

I have modeled this study on Viereck's research (1966), which followed the methods of Jenny (1941), Major (1951), and Crocker (1952). Jenny proposed that soil is the result of five independent variables—climate, organisms, topography, parent

material, and time—all acting together to produce a characteristic type of soil. He emphasized the value of finding examples in nature where all the variables but one are relatively constant. In his terminology, for example, a chronosequence develops with all factors except time held constant.

Major (1951) pointed out that these variables are just as valuable in vegetational studies, and illustrated a series of vegetation sequences in which all variables except one were kept constant.

Crocker (1952) suggested that the ecosystem would be a more logical unit to use than either soil or vegetation, for it is the ecosystem that is the function of the five independent variables. The present study is based on this concept. In addition, I have employed the principle of succession, which states that given an adequate period of time and barring disturbance, unstable ecosystems with the same climate, potential organisms, relief, and parent material will converge towards a single climax type.

Through reconnaissance studies and inspection of aerial photos, a selection was made of several young postburn stands (i.e., concrete ecosystems of Marr, 1961) of different ages and of two much older, relatively stable ecosystems. A permanent sample area, visually determined to be representative of each stand, was established, and a species list for it was compiled. The line intercept method (Canfield, 1941) and the macroplot method (Poulton and Tisdale, 1961) were used. Both methods are based on the line transect, although the latter adds small rectangular quadrats, called observation plots, for estimating herbaceous cover.

Ten parallel, 50-foot lines, each subdivided into 10-foot units, were laid out in each sample area at 25-foot intervals along a base line. Tree and shrub canopies projected onto these lines provided a measure of the relative importance or dominance of each species in the sample. According to Lindsey (1956), this canopy coverage is "the most important single parameter of a species in its community relations." Earlier studies of the pinyon-juniper type have also used the intercept technique (Cable, 1957; Jameson, Williams, and Wilton, 1962; and Arnold, Jameson, and Reid, 1964). Frequency, expressed as the percentage of subsamples in which a species occurs, was used to measure the relative distribution throughout the stand.

Understory was studied within 1x2-foot observation plots placed at 10-foot intervals along each line. Cover within these quadrats was estimated by using the Domin scale (Cain and Castro, 1959).

The abundance and reproduction of pinyon pine and juniper were compared by counting those individuals found within ten 4x50-foot belt transects adjacent to each line. The following size categories were used: seedlings, less than 1 foot in height; saplings,

stem diameters less than 2 inches; and trees, greater than 2 inches in diameter.

In the climax-forest samples, trees were selected for importance values and associated data, using the point quarter method of Cottam and Curtis (1956). Ten points were located at 50-foot intervals.

Tree-ring samples were dated according to the Douglass system (Glock, 1937). Increment cores provided ages of the recovering forest, while cross sections from charred snags were collected from the Long Mesa Burn to establish the date of that fire. Robert F. Nichols, archeologist and dendrochronologist with the Wetherill Mesa Project, helped collect samples from both the Long Mesa Burn and the Ute area climax forest. David G. Smith, dendrochronologist-climatologist formerly with the Laboratory of Tree-Ring Research, provided most of the dates.

Dating mature junipers was not attempted because this species often has an extremely erratic growth and lobing habit, and shows frequent doubling of rings.

Up-to-date discussions of the principles and applications of dendrochronology have been published by Bannister (1963), McGinnies (1963), and Fritts (1965a). A good treatment of "signature groups" and key years that occur in the Mesa Verde chronology is to be found in an article by Spencer (1964).

Soil profiles were described and additional information was provided by Orville Parsons, of the Soil Conservation Service. Where possible, photographs of these profiles were made by Fred Mang, Jr.

RESULTS

The Morfield Burn of 1959: Pioneer Weeds and Meadow Seral Stages

Between July 15 and August 7, 1959, a lightning-sparked fire burned 2,043 acres extending over sections of both Mesa Verde National Park and Ute Reservation lands of the east end of Mesa Verde. The flanks of the burn generally paralleled Morfield Canyon on the west and Whites Mesa to the east (Fig. 1).

Razing of the vegetation was complete (see frontispiece). After spending several days on a fire line at Whites Mesa, the fire crew was relieved from duty, and as we drove through the moonlit pall of ash and smoke in Waters Canyon the tree snags glowed like a myriad of campfires.

Some of the burned area had not been completely forested prior to the fire. Much of the eastern part of the park is covered with dense brush and scattered young pinyon and juniper trees. This vegetation has developed since the mid-1800's, when a large fire swept over the terrain. The western part of the Morfield Burn had been a pinyon-juniper forest with trees up to 30 feet in height. On an isolated ridge of this portion of the burn (Fig. 1) a permanent study

plot was established to monitor the vegetation change.

Vegetation.

According to park files, a mixture of commercial seed was air-dropped over most of the burned area in early October 1959, to check erosion. Equal amounts of intermediate wheatgrass (*Agropyron intermedium*), crested wheatgrass (*A. desertorum*), and smooth brome (*Bromus inermis*) were applied at the rate of 6 pounds per acre. The small ridge in Figure 1 was not seeded intentionally so that natural succession could be studied. But, because of seed drift, the exotic grasses soon became well established in the sample plot also. In order to promote tree recovery, 30 pounds of pinyon seeds were planted in a 1-acre plot on Whites Mesa. However, germination and growth have been poor.

The vegetation was leveled by the fire except for the snags of the mature trees. A layer of ash was evident over most of the landscape. But by autumn, many of the fire-adapted shrubs were sprouting from root crowns, and these were developing vigorously the following year. Gambel oak had crown-sprouted and was in leaf within a few months after the fire—impressive evidence of its adaptability to fire.

The pioneer vegetation during the first two years of recovery was dominated by two annuals, sunflower (*Helianthus annuus*) and pigweed (*Chenopodium pratericola*). Other adventives found at the site in 1960 were wheat (*Triticum aestivum*) and the brome grasses, *Bromus carinatus* and *B. japonicus*.

Further evidence suggests that the *Helianthus-Chenopodium* community-type constitutes an early seral stage throughout Mesa Verde. In the summer of 1960, a small plot on Chapin Mesa was intentionally burned in a fire-school demonstration. Sunflower and pigweed appeared the following year.

By 1962, the third year after the Morfield burn, the introduced and native grasses began supplanting the pioneer annuals. In August 1963 the grass community in the study plot was analyzed for cover and frequency, using the modified line intercept-macroplot method (Table 2). The grasses by then were well established, with scattered clumps of resprouted shrubs assuming a minor role (Fig. 2). The composite, *Machaeranthera bigelovii*, and Russian thistle (*Salsola kali*) were the most abundant forbs, but the original pioneer annuals were evident only as litter. Of the herbs listed in Table 2, only lupine (*Lupinus caudatus*) and *Penstemon linarioides* are components of the climax forest. The following perennial herbs, also common in the climax forest, were observed in the study area by 1963 but did not occur in the sample plot: *Poa fendleriana*, *Sitanion hystrix*, *Yucca baccata*, *Petradoria pumila*, *Opuntia polyacantha*, *Comandra umbellata*, *Arabis selbyi*, and *Eriogonum racemosum*. A summary of all the species occurring in the stands sampled is given in Table 13.

TABLE 2
COVER AND FREQUENCY OF THE
VEGETATION IN THE MORFIELD
BURN SAMPLE
ELEVATION 7,550 FEET. AUGUST, 1963

Species	% Cover	% Frequency*
Shrubs		
<i>Amelanchier utahensis</i> **	****	2
<i>Fendlera rupicola</i>	+	2
<i>Quercus gambelii</i>	+	2
Herbs		
<i>Machaeranthera bigelovii</i>	<4	74
<i>Agropyron desertorum</i>	<4	60
<i>Salsola kali</i>	<4	46
<i>Bromus tectorum</i>	<4	42
<i>Agropyron intermedium</i>	<4	34
<i>Viguiera multiflora</i>	<4	18
<i>Bromus inermis</i>	<4	10
<i>Oryzopsis hymenoides</i>	<4	6
<i>Descurainia pinnata</i>	+	44
<i>Lactuca scariola</i>	+	14
<i>Lappula redowskii</i>	+	8
<i>Lupinus caudatus</i>	+	8
<i>Chenopodium fremontii</i>	+	6
<i>Penstemon linarioides</i>	+	6
<i>Sphaeralcea coccinea</i>	+	6
<i>Camelina microcarpa</i>	+	4
<i>Moldavica parviflora</i>	+	2
Ground		
soil	25-33	92
litter	4-10	100
rock	<4	46

*Based on 50 subplots.

**Species authorities are given in the synoptical list of Table 13.

***Indicates presence but no significant cover value.

Soils.

The soils on the study ridge are highly variable. Parsons considered the soil just north of the sample plot to be Witt loam developing on a thin mantle of loess sediments over Cliffhouse sandstone. This pocket of relatively deep soil (one auger hole reached 60 inches to bedrock) is more like the eolian soils common at lower elevations to the south, where the mesa tops are broad and subject to less erosion.

The shallower soil south of the plot is Montvale stony fine sandy loam. No description was made of the profile, but the following data were obtained from auger holes at the corners of the macroplot: southeast corner 16 inches to bedrock, B₂ at 6 inches, + test for CaCO₃ at 12 inches depth; southwest corner 12 inches to bedrock, rock slabs at 8 inches, CaCO₃ test -; northwest corner 17 inches to bedrock, slight + CaCO₃ test at bottom, B₂ among

rock fragments; northeast corner 12 inches to bedrock, CaCO_3 test + at bottom. Rock outcrops occur along the edges of the ridge and in parts of the sample plot.

In general, the soil within the macroplot is probably less than two feet in depth. Some CaCO_3 occurs at the bedrock-soil interface.

The Wetherill Burn of 1934: the Mountain
Brush Seral Stage

Biesen (1931) prefaced his description of the conifers of Mesa Verde with these observations:

While the trees of the park completely cover the mesa areas, they do not grow densely together. . . For this reason as well as for the fact that usually heavy downpours accompany each severe electrical storm, the fire hazard of the park is not considered to be very great. It is interesting to note that Mesa Verde has not been troubled with severe fires in recent years. During the present season



Fig. 2. Aspect of the Morfield Burn in July 1963. The vegetation at this stage consists of exotic and native grasses, some forbs, and scattered fire-adapted shrubs, such as this small clone of Gambel oak in the foreground. Soils on this ridge are variable. Elevation, 7,500 feet.

only two small fires have been reported, and they were quickly extinguished by the Park's efficient protective organization.

This was the feeling that prevailed in the park prior to 1934. Fire was never considered a serious threat to the mantle of pinyon-juniper, often referred to as "the asbestos forest."

That view soon changed when the largest fire in park history taxed the efforts of over 1,000 men attempting to control it. Don Watson (1934), then ranger-historian of the park, gave this account of the event:

On the ninth of July a small cloud, wandering across the Mesa Verde, caused an electrical storm that sent a few streaks of lightning down into our forests. One of these lightning streaks, striking a tree, started a fire that was to prove the most disastrous Mesa Verde has ever known. For two weeks it raged, ultimately consuming 4,540 acres of timber and brush lands.

The Wetherill Burn was in reality the result of two fires that flared up consecutively, one on the Ute Mountain Indian Reservation on July 9, and the other in the park on July 11, 1934. During a flare-up on July 14, they merged into a fire that was not declared out until July 26. This burn, too, left a desolate landscape in its wake.

The following incident provides further evidence of the fire potential of lightning. An extremely abbreviated electrical storm that resulted in a "smoke" occurred one summer afternoon in 1964 while I was visiting Long House, a cliff dwelling on Wetherill Mesa. The weather was fair with no sign of shower activity. Yet while I was in the recesses of the large rock shelter I heard what later proved to have been a lightning bolt strike a large juniper tree about 1 mile up the mesa. The fire was quickly suppressed before it spread, but this event underscores the major role of fire in the dynamics of the regional vegetation prior to modern fire-fighting technology.

Contrary to the statement of Biesen (1931), electrical storms are a consequential factor in determining the nature of the Mesa Verde vegetation. The Wetherill Burn, and, more recently, the Morfield fire were lightning-caused.

Vegetation.

As with the Morfield Burn, attempts to reforest the area artificially have met with but limited success. There were 42,000 trees planted on Wetherill Mesa in 1942 (unpublished park records). Several years earlier, the Civilian Conservation Corps planted 200,000 seedlings. Only a few isolated stands of these pinyon

pinos and Rocky Mountain junipers (*Juniperus scopulorum* Sarg.) persist today, in most cases as rows across shallow washes off the main ridges.

The present open brush vegetation was sampled in 1963 in an area heavily forested before the 1934 fire (Fig. 3). A macroplot was established on the main ridge of Wetherill Mesa at an elevation of 7,650 feet (Fig. 1). The data given in Table 3 are for only those plants intercepted by the sample lines or included in

TABLE 3
COVER AND FREQUENCY OF THE
VEGETATION IN THE WETHERILL
BURN SAMPLE
ELEVATION 7,650 FEET, AUGUST, 1963

Species	% Cover	%Frequency*
Trees		
<i>Pinus edulis</i>	***	2
Shrubs		
<i>Amelanchier utahensis</i>	10	20
<i>Yucca baccata</i>	6	16
<i>Chrysothamnus nauseosus</i>	2	10
<i>Cercocarpus montanus</i>	1	6
<i>Fendlera rupicola</i>	1	6
<i>Symphoricarpos oreophilus</i>	+	4
Herbs		
<i>Poa fendleriana</i>	4-10	88
<i>Sitanion hystrix</i>	<4	24
<i>Sphaeralcea coccinea</i>	<4	22
<i>Heterotheca villosa</i>	<4	18
<i>Bromus tectorum</i>	+	22
<i>Penstemon linarioides</i>	+	16
<i>Schoenocrambe linifolium</i>	+	16
<i>Lappula redowskii</i>	+	10
<i>Viguiera multiflora</i>	+	8
<i>Polygonum racemosum</i>	+	6
<i>Zygademus elegans</i>	+	6
<i>Petradoria pumila</i>	+	6
<i>Oryzopsis hymenoides</i>	+	6
<i>Moldavica parviflora</i>	+	4
<i>Comandra umbellata</i>	+	4
<i>Machaeranthera bigelovii</i>	+	4
<i>Stipa comata</i>	+	2
<i>Lupinus caudatus</i>	+	2
<i>Calochortus nuttallii</i>	+	2
<i>Achillea lanulosa</i>	+	2
<i>Arabis selbyi</i>	+	2
Ground		
soil	25-33	88
litter	4-10	96
rock	<4	20

*Based on 50 subplots.
**Indicates presence but no significant cover value.



Fig. 3. Aspect of the Wetherill Burn in July 1963. Dead snags of the former pinyon-juniper forest show little weathering. The mountain-brush species, released from competition with the trees, are becoming more dominant. Elevation, 7,650 feet.

the observation plots. Gambel oak, for example, was not sampled but was abundant along the edges of the ridge. Bitterbrush (*Purshia tridentata*), too, was common in the burn but not in the immediate area. A listing of those species occurring in the macroplot area, however, is given in Table 13.

The stand was characterized by serviceberry (*Amelanchier utahensis*), *Yucca baccata*, *Poa fendleriana*, and *Heterotheca villosa*. One pinyon pine sapling occurred in the macroplot and was included in the line intercept. Since the pith date by ring count was 1953, this tree was not part of the earlier planting program. Such a delay in natural establishment of the tree component is consistent with the postfire recovery on Mesa Verde. Regardless of the extent of the area burned, 20 to 30 years usually lapse before the pinyon-juniper element begins to return.

The few nonvascular plants encountered are, for the most part, the moss *Grimmia*, found on rocks scattered over the ridge. A small complex of lichens,

principally *Collema tenax*, covers parts of the soil surface.

Soil.

The soil profile (Fig. 4 and Table 4) was studied at a pit located a short distance down the ridge from the macroplot. According to Parsons (personal communication), the soil representative of this site is tentatively identified as Roubideau very fine sandy loam. It has developed primarily from weathered products of the underlying sandstone, although eolian soils have modified it to some extent. Soil depth around the macroplot, however, is shallower. Holes augered at the corners of the sample revealed the following depths to bedrock: southeast corner, 14 inches; southwest corner, 10 inches; northwest corner, 6 inches; and northeast corner, 6 inches. Tests for CaCO_3 were negative. Several additional test holes inside the macroplot ranged from 20 to 43 inches in depth. One of these had 10 inches of caliche (CaCO_3) in the lower part of the profile.



Fig. 4. Soil profile underlying the Wetherill Burn near the macroplot sample. The soil in this pit typifies the Roubideau very fine sandy loam. Note the deep, highly structured B₂ horizon and the absence of CaCO₃.

TABLE 4
DESCRIPTION OF THE SOIL PROFILE
UNDERLYING THE WETHERILL BURN
NEAR THE MACROPLOT SAMPLE

Horizon	Depth (inches)	Description
A ₁₁	0-4	Brown (7.5YR 5/2, dry) to dark brown (7.5YR 3/2, moist) very fine sandy loam; moderate to strong very fine granular structure; consistence soft dry, very friable moist; noncalcareous; weakly platy structure in the upper inch or two; lower boundary clear and smooth.
A ₁₂	4-7	Reddish-brown (5.0YR 5/3, dry) to reddish-brown (5.0YR 4/3, moist) very fine sandy loam; weak medium structure breaking to weak to
B ₁	7-12	moderate medium subangular blocks; consistence slightly hard dry, and very friable moist; many fine pores, numerous fine worm casts; noncalcareous; lower boundary clear and smooth.
B ₂₁	12-19	Reddish-brown (5.0YR 5/4, dry) to dark reddish-brown (5.0YR 3/4, moist) heavy loam; moderate medium prismatic structure breaking to moderate medium subangular blocks; consistence hard dry, and very friable moist; a few very thin and patchy clay skins on soil peds, noncalcareous; lower boundary clear and smooth.
B ₂₂	19-32	Reddish-brown (slightly redder than 5.0YR 5/4, dry, and 5.0YR 4/4, moist) heavy clay loam; strong medium prismatic structure breaking to strong medium angular blocks; consistence very hard dry, and firm moist; thin almost continuous clay skins on soil peds; slickenside numerous; noncalcareous; lower boundary clear and smooth.
R	32	Relatively unweathered sandstone with extensions of B ₂₂ into cracks.

The Long Mesa Burn of 1873: the Mountain
Brush-Incipient Forest Seral Stage

Long Mesa lies due east of Wetherill Mesa (Fig. 1). Its northern ridges are within the area of the 1934 Wetherill Burn. Much of the northern part of Long Mesa and a large segment of Long Canyon show evidence of a fire that occurred before the park was established. To my knowledge, this burn antedates the settling of the region by early ranchers.

A site was selected on a narrow ridge where the fire, originating in Long Canyon, had spread over part of the mesa top (Fig. 1). This small section of the Long Mesa Burn was bordered on the north and south by pinyon-juniper forest.

Dating the Burn.

Cross sections were cut from pinyon pines that had been killed by the fire. The results given in Table 5 indicate that the event must have occurred *after* 1870. This was not a bark date since the terminal rings had weathered away, and the date presumably represents the latest date of the outermost persisting rings.

TABLE 5

OUTSIDE RING DATES OF PINYON PINES
KILLED IN THE LONG MESA BURN OF 1873

Mesa Verde Specimen No.	Outside Ring Date
3002	1870
3003	1810±
3004	c.1846
3005	no date
3009	1868
3011	no date
3015	no date
3016	no date
3019	1869
3020	c.1860

The most recent year in which the fire might have occurred is 1896. This is the pith date of the oldest living tree within the burn. This second line of evidence—increment cores from trees that have come in subsequent to the fire (Table 6)—provided the latest dates possible for the burn.

More precision was made possible by studying two Douglas-fir trees that were caught in the upward

TABLE 6

DATES FOR PINYON-JUNIPER ESTABLISHMENT
FOLLOWING THE LONG MESA BURN OF 1873

Mesa Verde Specimen No.	Species	Inside Ring Date ¹
3047	Utah juniper	1896±nc ²
3048	Utah juniper	1908 nc
3055	pinyon pine	1927 p ³
3056	pinyon pine	1901 p
3057	pinyon pine	1912 nc
3058	pinyon pine	1907 nc
3059	pinyon pine	1907 nc
3060	pinyon pine	1900 p
3063	pinyon pine	1905 p
3064	pinyon pine	1900±nc
3065	pinyon pine	1912 nc

¹Based on increment cores

²nc indicates "near center"

³p indicates "pith"

sweep of the fire as it moved out of Long Canyon. A wedge (Mesa Verde specimen No. 3066) was cut from one of the trees destroyed by the fire. The ring series from this section was plotted and matched with the master chronology developed for Mesa Verde by dendrochronologists of the Laboratory of Tree-Ring Research (Fig. 5). The pith date was 1663; the extremely eroded outermost ring was 1871 (Fig. 6), a date that was in accord with those from the mesa-top samples.

At the same time the wedge was collected, an increment core (Mesa Verde specimen No. 3067) was taken from a Douglas-fir tree that was living but had probably been affected by the fire. David Smith studied the core and arrived at a probable fire date of 1874 based on a suppression wood sequence from 1874 through 1889 (Fig. 7). Apparently no xylem increment occurred in the position from which the increment core was taken during the initial years, for only ten rings are evident in the suppression series.

In light of radial growth studies reported by Douglas and Erdman (1967) and a closer analysis of the increment core in Figure 7, the year 1873 may be a more accurate date of the Long Mesa fire. Radial growth in Douglas-fir terminates by late spring, certainly by early June. Therefore, the increment laid down the year of the fire should be normal, not locally absent or suppressed; 1873 is the last normal ring before the sequence, 1874 through 1889.

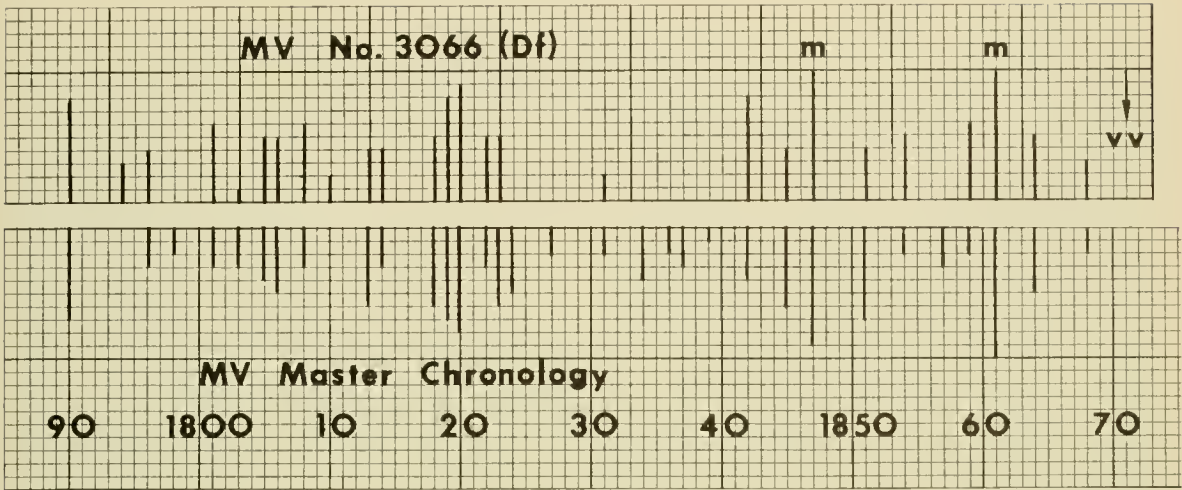


Fig. 5. Dating the Long Mesa Burn: Cross-dating the skeleton plot derived from the wedge of a burned Douglas-fir with the Mesa Verde master chronology. A diagnostic grouping, or "signature" occurs in the 1818-24 sequence. Other key years are 1847, 1851, and 1861. The annual increments for 1847 and 1861 are missing from the specimen (indicated by the letter m). The extremely eroded outermost ring of 1871 is indicated by the symbol vv.

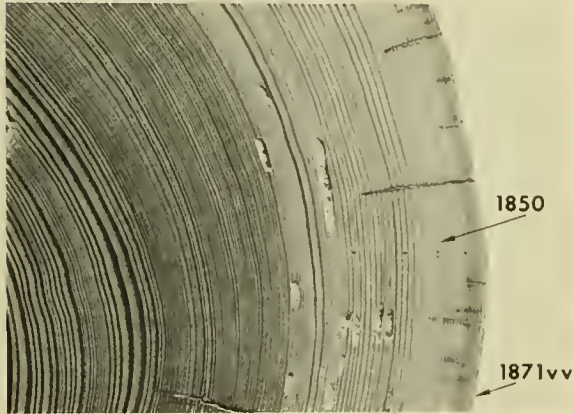


Fig. 6. Dating the Long Mesa Burn: Part of the wedge of a burned Douglas-fir (Mesa Verde specimen No. 3066) from which the skeleton plot shown in Figure 5 was made. The cross-dating provided an outermost ring date of 1871. The single pinholes indicate decades; the double pinhole, the 1850 increment.

Vegetation.

The present vegetation in the Long Mesa Burn is a dense entanglement of shrubs and young trees (Fig. 8). The dead, charred snags of the former forest are generally screened by this new vegetation.

The pinyon-juniper component of the stand has been increasing since the turn of the century, when the first seedlings were established (Table 6). Although the older trees are 15 to 20 feet in height, the mountain brush species continue to characterize the stand (Table 7). The shrubs with the maximum cover and greatest frequency were bitterbrush (*Purshia tridentata*) and *Fendlera rupicola*, both almost tree-like in their growth habits here, in contrast to their small size in the climax forest.

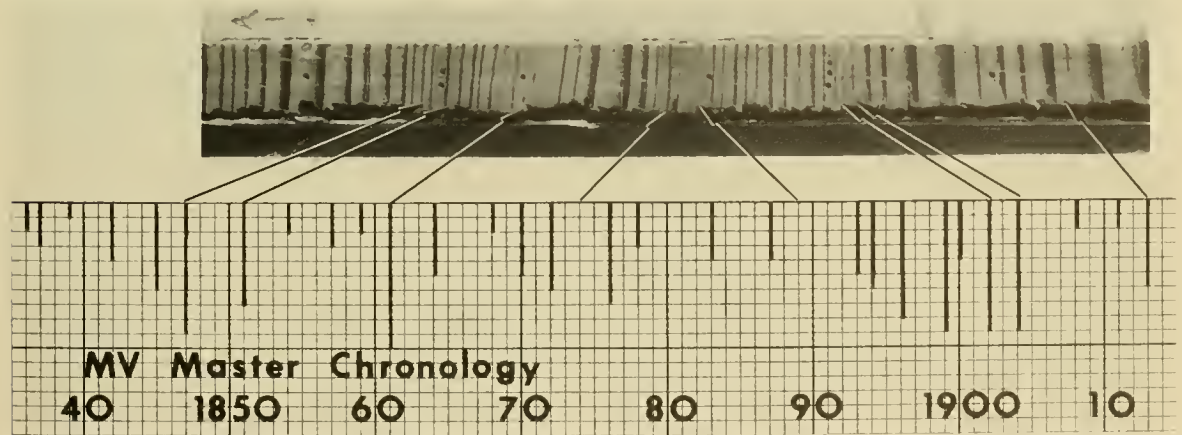


Fig. 7. Dating the Long Mesa Burn: Increment core of Douglas-fir cross-dated with the Mesa Verde master chronology. The length of each vertical bar on the graph is inversely proportional to the relative width of the ring; average width rings are not recorded. The suppression wood between the years 1874 and 1889 is atypical and reflects the effect of the fire. Micro-rings occurred in 1847, 1851, 1861, 1902, and 1904.



Fig. 8. Aspect of the Long Mesa Burn in July 1963. The mountain brush species dominate the stand although the cone-bearing pinyon-juniper canopy is overtopping them. The charred snag in the center was a mature Utah juniper. Elevation, 7,400 feet.

Most of the herbs sampled were perennials, the only exceptions being *Polygonum sawatchense*, found in the pinyon-juniper forest throughout Mesa Verde, the widespread cheatgrass (*Bromus tectorum*), and the almost equally common weed, *Lappula redowskii*.

Soil.

The soil underlying the burn is identified as a shal-

low phase of Montvale fine sandy loam. It is very stony and highly calcareous, as is evident in Figure 9. Eolian sediments are possibly a minor influence in this solum, developing residually from weathered Cliffhouse sandstone.

Plant growth may be enhanced by the underlying fractured sandstone, which serves as a reservoir for additional soil moisture, and by some lateral flow along the bedrock surface.

TABLE 7

COVER AND FREQUENCY OF THE VEGETATION
IN THE LONG MESA BURN SAMPLE
ELEVATION 7,400 FEET. SEPTEMBER, 1963

	Species	% Cover	% Frequency*
Trees			
	<i>Pinus edulis</i>	19	46
	<i>Juniperus osteosperma</i>	6	12
Shrubs			
	<i>Purshia tridentata</i>	26	82
	<i>Fendlera rupicola</i>	14	48
	<i>Yucca baccata</i>	13	40
	<i>Cercocarpus montanus</i>	2	10
	<i>Quercus gambelii</i>	+**	4
	<i>Amelanchier utahensis</i>	+	2
Herbs			
	<i>Poa fendleriana</i>	<4	56
	<i>Lappula redowskii</i>	<4	32
	<i>Oryzopsis hymenoides</i>	<4	16
	<i>Opuntia polyacantha</i>	<4	6
	<i>Eriogonum umbellatum</i>	<4	6
	<i>Bromus tectorum</i>	+	22
	<i>Penstemon linarioides</i>	+	16
	<i>Sitanion hystrix</i>	+	8
	<i>Senecio multilobatus</i>	+	6
	<i>Bouteloua gracilis</i>	+	4
	<i>Cryptantha bakeri</i>	+	4
	<i>Polygonum sawatchense</i>	+	4
	<i>Artemisia ludoviciana</i>	+	2
	<i>Schoenocrambe linifolium</i>	+	2
	<i>Gutierrezia sarothrae</i>	+	2
	<i>Sphaeralcea coccinea</i>	+	2
	<i>Petradoria pumila</i>	+	2
	<i>Penstemon strictis</i>	+	2
Ground			
	litter	25-33	100
	soil	10-25	46
	rock	<4	36

*Based on 50 subplots.

**Indicates presence but no significant cover value.

This profile is similar to the profile described in the climax forest nearby (Table 11), although the former is four inches less in total depth and has a slightly coarser-textured B₂ horizon.

The Long Mesa Climax Site: the
Pinon-Juniper/Mountain Brush Stage

One mile north of the Long Mesa Burn lies a small stand of pinon-juniper that was missed by both the



Fig. 9. Soil profile underlying the Long Mesa Burn. This soil is transitional between Montvale fine sandy loam and shallower series. The highly structured, blocky B₂ is developing between fragments of Cliffhouse sandstone which overly a pronounced C_{ea} horizon.

1873 and 1934 fires (Fig. 1). This stand was studied for two reasons. First, as a remnant of the forest that was destroyed in the 1873 burn, it served as a control. Secondly, and of more significance, it is considered to be representative of the type of vegetation that can develop on relatively shallow soils in the Mesa Verde only after centuries of little disturbance—the climax forest-type under the present climatic regime.

Vegetation.

This 400-year-old stand consists of but a few characteristic species. Those apparent in Figure 10 are *Yucca baccata*, *Poa fendleriana*, the prickly-pear, *Opuntia polyacantha*, and some scraggy examples of the mountain brush element.

On the basis of the macroplot analysis (Table 8), the pinon pine and Utah juniper are clearly codominants, with similar cover values and frequencies. But from the results given in Table 9, juniper is more dominant than pinon pine, and is of considerably more importance in the stand. These differences are due to differences in the criterion used to determine dominance. The macroplot method stresses cover from the canopy; the point quarter method summarized in Table 9 emphasizes board feet. Cover was

based on canopy projection irrespective of tree size; the point quarter study excluded trees less than four inches in diameter. Pinyon pine had a relatively small trunk compared with juniper, averaging seven inches in diameter. Trunks of juniper averaged 20 inches. The density transects reported in Table 10 indicate

that pinyon pine was more numerous when seedlings and saplings are considered. Thus, although juniper was the aspect dominant, pinyon pine was more abundant. Both species attained crown heights of 35 feet, about the maximum reported for other parts of the Mesa Verde.



Fig. 10. Aspect of the Long Mesa climax stand in July 1963. The sparse understory consists mostly of *Poa fendleriana*, *Yucca baccata*, and generally suppressed shrub species such as the mountain mahogany in the foreground. Elevation, 7,600 feet.

The age of the stand was based upon increment cores taken from the older trees in the stand. The oldest pith ring date, 1576, came from a 21-inch diameter pinyon. The considerably greater diameters of juniper trunks, however, suggest that this species may be the older of the tree components. Unfortunately, mature juniper trees can rarely be dated.

TABLE 8

COVER AND FREQUENCY OF THE VEGETATION
IN THE LONG MESA CLIMAX FOREST
ELEVATION 7,600 FEET. AUGUST, 1963

Species	% Cover	% Frequency*
Trees		
<i>Juniperus osteosperma</i>	31	50
<i>Pinus edulis</i>	27	48
Shrubs		
<i>Cercocarpus montanus</i>	14	28
<i>Yucca baccata</i>	2	14
<i>Symphoricarpos oreophilus</i>	2	12
<i>Fendlera rupicola</i>	2	8
<i>Amelanchier utahensis</i>	++	2
<i>Purshia tridentata</i>	+	2
Herbs		
<i>Poa fendleriana</i>	4-10	80
<i>Penstemon linarioides</i>	<4	24
<i>Opuntia polyacantha</i>	<4	10
<i>Comandra umbellata</i>	+	14
<i>Eriogonum umbellatum</i>	+	8
<i>Petradoria pumila</i>	+	8
<i>Polygonum sawatchense</i>	+	6
<i>Schoenocrambe linifolium</i>	+	6
<i>Lupinus ammophilus</i>	+	4
<i>Oryzopsis hymenoides</i>	+	4
<i>Lappula redowskii</i>	+	4
<i>Bromus tectorum</i>	+	4
<i>Sitanion hystrix</i>	+	2
<i>Pedicularis centranthera</i>	+	2
<i>Cryptantha bakeri</i>	+	2
<i>Chenopodium fremontii</i>	+	2
<i>Balsamorhiza sagittata</i>	+	2
Ground		
litter	33-50	94
soil	4-10	48
rock	<4	20

*Based on 50 subplots.
**Indicates presence but no significant cover value.



Fig. 11. Soil profile underlying the Long Mesa climax stand. The Montvale fine sandy loam has a finer-textured B horizon than is typical, but otherwise it is representative.

Soil.

This soil, too, has been tentatively identified as Montvale fine sandy loam. It has a finer-textured B horizon than is typical of most of the Montvale soils mapped in the area by Parsons (MS), but it is otherwise representative. The CaCO₃ component is less extensive than that in the burn sample. The profile (Fig. 11) is described in Table 11.

Additional Evidence on Climax: Ute
Pinyon-Juniper/Mountain Brush Forest

An answer to the problem of determining climax vegetation is especially difficult in the park proper because prehistoric burns cover the entire northern third of its area. On the other hand, the Ute Indian holdings of the Mesa Verde to the west remain relatively unaffected by fire. For whatever reason, a mature pinyon-juniper forest covers that section of the mesa. The mountain brush or chaparral "zone" so familiar in the park is not evident on the Reservation.

In 1963, a reconnaissance flight over Mesa Verde prompted a brief excursion into the reservation forest. On July 11, 1964, a small field party ascended the North Rim in the vicinity of the Mesa Verde Mine, about four miles west of Wetherill Mesa. A

TABLE 9

POINT QUARTER ANALYSIS OF THE PINYON-JUNIPER ELEMENT IN THE LONG MESA CLIMAX FOREST*

Species	Number of Trees	Mean Distance (feet)	Basal Area (inches ²)	Density No./Acre	Dens. (%)	Relative Freq. (%)	Dom. (%)	Importance Value (D+F+Do)
<i>Juniperus osteosperma</i>	24	-	7,309	155	60	53	92	205
<i>Pinus edulis</i>	16	-	647	103	40	47	8	95
all trees	40	13	7,956	258	100	100	100	300

*Sampling method included only those trees greater than four inches in diameter.

TABLE 10

TREE DENSITY ANALYSIS OF THE LONG MESA CLIMAX FOREST BASED ON TEN 4x50-FOOT BELT TRANSECTS

Species	Seedlings*	Saplings**	Trees***	Total
<i>Pinus edulis</i>	6	10	8	24
<i>Juniperus osteosperma</i>	5	0	9	14

*Individuals less than one foot in height.

**Individuals taller than one foot but with the main stem less than two inches in diameter.

***Individuals with main stems greater than two inches in diameter.

pinjun-juniper stand with a mountain-brush understory similar to the one studied on Long Mesa was selected for observation (Fig. 12). The elevation of this ridge-top site was 7,900 feet.

The species composition was generally similar to that in the Long Mesa climax stand, except for some herbs along the North Rim in the park.

The tree stratum was very similar to that on Long Mesa, although the Ute stand tended to be more open (Table 12). Maximum height was 35 feet and the approximate age was 400 years. One of the largest pinyon pines observed in the Mesa Verde was cored at this site; the diameter was 32 inches, and the date of the center ring was 1539. Several other pinyons dated around 1600. A Utah juniper, 20 feet tall and 15 inches in diameter was also cored. The center ring



Fig. 12. Detail of the pinyon-juniper/mountain brush element that characterizes the higher parts of the Mesa Verde in the Ute Mountain Indian Reservation. Elevation at this ridge-top site is 7,900 feet.

date was 1570, nearly as old as the pinyon of twice the size. The largest juniper in the point quarter analysis was 36 inches in diameter. These data, along with similar results obtained elsewhere, suggest that the juniper component in much of the forested sections of the Mesa Verde is considerably older than the pinyon pine codominant.

TABLE 11

DESCRIPTION OF THE SOIL PROFILE
UNDERLYING THE LONG MESA CLIMAX FOREST

Horizon	Depth (inches)	Description
A ₁	0-4	Brown (7.5YR 5/3, dry) to dark brown (7.5YR 3/3, moist) fine sandy loam; moderate to strong very fine granular structure; consistence soft dry, and very friable moist; considerable dark organic flakes and very many fine almost matted roots; non-calcareous; lower boundary clear and smooth.
B ₁	4-7	Brown (slightly redder than 7.5YR 5/4, dry) to dark brown (slightly redder than 7.5YR 3/4, moist) loam; weak medium sub-angular structure; consistence slightly hard dry, and very friable moist; very many fine roots and pores; noncalcareous; lower boundary clear and smooth.
B ₂₁	7-10	Brown (slightly redder than 7.5YR 5/4, dry) to dark brown (slightly redder than 7.5YR 3/4, moist) heavy loam; weak medium prismatic structure breaking to moderate medium angular blocky structure; consistence very hard dry, and very friable moist; thin patchy clay skins; many fine roots,

Table 11 (Continued)

		numerous cicada casts, 5 percent weathered sandstone chips; non-calcareous; lower boundary clear and smooth.
B ₂₂	10-14	Reddish-brown (5.0YR 5/4, dry) to reddish-brown (5.0YR 3/4, moist) clay loam; moderate medium prismatic structure breaking to strong medium and fine angular blocky structure; consistence very hard dry, and firm to slightly friable moist; almost continuous clay skins with some slickensides; 25 percent weathered sandchips; non-calcareous; lower boundary clear and smooth.
B _{3ca}	14-16	Brown (7.5YR 5/4, dry) to dark brown (7.5YR 4/4, moist) heavy loam or light clay loam; weak medium subangular blocky structure; consistence hard dry, and friable moist; white chalky lime concretions, 25 percent sandstone fragments; very thin patchy clay skins; strongly calcareous; lower boundary clear and smooth with large roots following along underlying sandstone surface.
R	16	Relatively indurated sandstone.

TABLE 12

POINT QUARTER ANALYSIS OF THE PINYON-JUNIPER ELEMENT IN THE
UTE MOUNTAIN INDIAN RESERVATION CLIMAX FOREST*

Species	Number of Trees	Mean Distance (feet)	Basal Area (inches ²)	Density No./Acre	Dens. (%)	Relative Freq. (%)	Dom. (%)	Importance Value (D+F+Do)
<i>Juniperus osteosperma</i>	27	—	9,020	61	68	56	81	205
<i>Pinus edulis</i>	13	—	2,111	29	32	44	19	95
all trees	40	22	11,131	90	100	100	100	300

*Sampling method included only those trees greater than four inches in diameter.

Dendrochronology: A New Application

The counting of rings from actively growing trees has been used for years to determine the age of forest stands and even some geomorphological events. For instance, ring counts have provided some information on the effects of fire and other disturbances on the pinyon-juniper type in Arizona (Arnold, Jameson, and Reid, 1964). This simple dating technique is not usable, however, in dating fires because we do not know how soon living trees become established after burns (Fig. 13). On the other hand, the method of cross-dating specimens directly affected by a fire with a master chronology for the region can provide rather accurate dating information.



Fig. 13. A pinyon pine began growing in the burned-out base of a juniper about 1880, and thereby established a baseline from which to work back in time to determine the date of the fire. This site is on Big Mesa in the eastern part of the Mesa Verde. An 18-inch increment borer provides a scale.

In the Mesa Verde, for example, the northern ridge of Moccasin Mesa is covered with a scattering of young pinyon-junipers, most of which were established around the turn of the present century. All the charred specimens collected for dating purposes, however, placed the burn in the 18th century. Perhaps recurrent flash fires prevented the return of pinyon-junipers for almost a century. In any event, this information would not have been available from simple ring counts.

In summary, where master chronologies are available or can be built, cross-dating trees destroyed or otherwise affected by fire provides reliable data concerning the time of the disturbance. This technique might well be applied to other ecological work of this sort.

DISCUSSION AND CONCLUSIONS

Pinyon-Juniper Succession after Fires on Residual Soils of Mesa Verde

In Mesa Verde sites where dense stands of pinyon-juniper on shallow, residual soils have been burned, recovery begins with the establishment of annuals, which reach a maximum density in two to three years. *Helianthus* and *Chenopodium* are the initial dominant pioneers, followed by Russian thistle (*Salsola kali*) and *Machaeranthera bigelovii*. By the fourth year perennial grasses dominate the burn. Under natural conditions, these consist of Indian ricegrass (*Oryzopsis hymenoides*), muttongrass (*Poa fendleriana*), and squirreltail (*Sitanion hystrix*). The grass and forb stage eventually gives way to a persistent mountain-brush vegetation type. This postfire sere is generally consistent with the one reported by Arnold, Jameson, and Reid (1964) in Arizona.

When fires recurred periodically in prehistoric times, a chaparral fire climax persisted along the upper reaches of Mesa Verde. But under the present protective regime, a young, open stand of trees is gradually suppressing the shrub element, and eventually a mature forest may again be established. These successional stages following a fire are given in Figure 14.

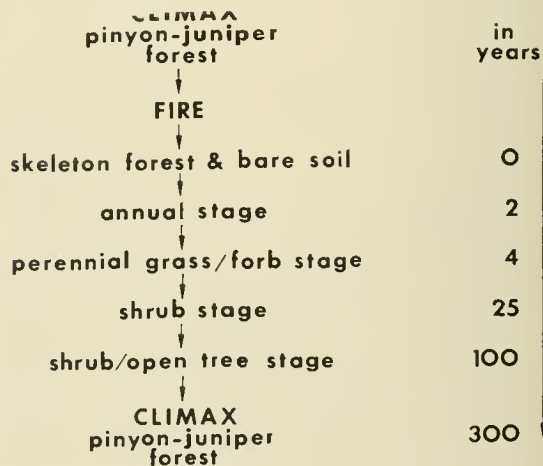


Fig. 14. Suggested successional stages after fire on residual soils of the Mesa Verde.

Details of species change in the postfire sere, summarized in Table 13, lead to the following conclusions. First, in the change toward a climax status there is a definite trend towards impoverishment in the floristic composition. In the young Morfield Burn community there were 47 species, compared to 40 in the older Wetherill Burn, 28 in the Long Mesa Burn, and 26 in the climax forest. This trend is due primarily to the reduction of weedy annuals and biennials.

TABLE 13
SPECIES LISTING BY COMMUNITY ACCORDING TO SUCCESSIONAL STATUS*

Species**	1959 Burn	1934 Burn	1873 Burn	Climax Forest
Trees				
<i>Pinus edulis</i> Engelm.		+	+	+
<i>Juniperus osteosperma</i> (Torr.) Little			+	+
Shrubs				
<i>Chrysothamnus nauseosus</i> (Pall.) Britt.	+	+		
<i>Quercus gambelii</i> Nutt.	+	+	+	+
<i>Amelanchier utahensis</i> Koehne	+	+	+	+
<i>Cercocarpus montanus</i> Raf.	+	+	+	+
<i>Fendlera rupicola</i> A. Gray	+	+	+	+
<i>Yucca baccata</i> Torr.	+	+	+	+
<i>Purshia tridentata</i> (Pursh) DC.		+	+	+
<i>Symphoricarpos oreophilus</i> A. Gray		+		+
Grasses				
<i>Agropyron desertorum</i> (Fisch.) Schult.	+			
<i>Agropyron intermedium</i> (Host.) Beauv.	+			
<i>Bromus carinatus</i> Hook. & Arn.	+			
<i>Bromus inermis</i> Leyss.	+			
<i>Bromus japonicus</i> Thunb.	+			
<i>Triticum aestivum</i> L.	+			
<i>Bromus tectorum</i> L.	+	+	+	+
<i>Oryzopsis hymenoides</i> (R. & S.) Ricker	+	+	+	+
<i>Poa fendleriana</i> (Steud.) Vasey	+	+	+	+
<i>Sitanion hystrix</i> (Nutt.) J. G. Smith	+	+	+	+
<i>Koeleria gracilis</i> Pers.		+		
<i>Stipa comata</i> Trin. & Rupr.		+	+	
<i>Bouteloua gracilis</i> (H.B.K.) Lag.			+	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray			+	
Subshrubs and Forbs				
<i>Helianthus annuus</i> L.	+			
<i>Chenopodium pratericola</i> Rydb.	+			
<i>Salsola kali</i> L.	+			
<i>Camelina microcarpa</i> Andr.	+			
<i>Descurainia pinnata</i> (Walt.) Britt.	+			
<i>Descurainia sophia</i> (L.) Webb. ex E. & P.	+			
<i>Melilotus officinalis</i> (L.) Lamb	+			
<i>Arabis selbyi</i> Rydb.	+			
<i>Astragalus scopulorum</i> T. C. Porter				
<i>Lithospermum ruderale</i> Dougl.	+			
<i>Cirsium</i> cf. <i>undulatum</i> (Nutt.) Spreng.	+	+		
<i>Lactuca scariola</i> L.	+	+		
<i>Machaeranthera bigelovii</i> (Gray) Greene	+	+		
<i>Moldavica parviflora</i> (Nutt.) Britt.	+	+		
<i>Tragopogon dubius</i> Scop.	+	+		
<i>Viguiera multiflora</i> (Nutt.) Blake	+	+		
<i>Erigeron flagellaris</i> A. Gray	+	+		
<i>Eriogonum racemosum</i> Nutt.	+	+		
<i>Heterotheca villosa</i> (Pursh) Shinnars	+	+		
<i>Lupinus caudatus</i> Kell.	+	+		+
<i>Zygadenus paniculatus</i> (Nutt.) Wats.		+		
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	+	+	+	
<i>Lappula redowskii</i> (Hornem.) Greene	+	+	+	+
<i>Polygonum sawatchense</i> Small	+	+	+	+
<i>Schoenocrambe linifolium</i> (Nutt.) Greene	+	+	+	+
<i>Balsamorhiza sagittata</i> (Pursh) Nutt.	+	+		+
<i>Comandra umbellata</i> (L.) Nutt.	+	+		+
<i>Opuntia polyacantha</i> Haw	+	+	+	+
<i>Penstemon linarioides</i> A. Gray	+	+	+	+
<i>Petradoria pumila</i> (Nutt.) Greene	+	+	+	+
<i>Senecio multilobatus</i> T. & G. ex A. Gray	+		+	
<i>Senecio mutabilis</i> Greene		+		
<i>Artemisia ludoviciana</i> Nutt.	+	+	+	

TABLE 13 (Continued)

<i>Gutierrezia sarothrae</i> (Pursh) B. & R.		+	+	
<i>Crepis</i> sp.	+			
<i>Cymopterus bulbosus</i> A. Nels.		+		
<i>Penstemon strictis</i> Benth. ex DC.			+	
<i>Cryptantha bakeri</i> (Greene) Payson			+	+
<i>Eriogonum umbellatum</i> Torr.			+	+
<i>Lupinus ammophilus</i> Greene				+
<i>Pedicularis centranthera</i> A. Gray ex Torr.				+

*Within groups pioneer plants are listed first while those more restricted to the climax forest are last.

**Nomenclature follows that of Welsh and Erdman (1964); more recent nomenclatural changes were provided by William A. Weber, University of Colorado Museum.

Inasmuch as several of the grasses listed in Table 13 are adventives, the permanency of those artificially seeded will require further study. *Poa fendleriana*, on the other hand, is the most characteristic grass in the Mesa Verde area and in much of the pinyon-juniper climax region of the Southwest.

All the shrubs listed, except rabbitbrush (*Chrysothamnus nauseosus*), are common in the pinyon-juniper/mountain-brush forests of the Southwest; and probably all of these, except rabbitbrush, reproduce in varying degrees by crown-sprouting. Resprouting of the bitterbrush (*Purshia tridentata*) was not observed, although it is known to sprout or stem layer in California (Nord, 1959). Snowberry (*Symphoricarpos oreophilus*) may propagate similarly, for it occurs in the fairly recent burn at Wetherill Mesa. Another species of snowberry, *S. rivularis*, crown-sprouts along coastal California (Wells, 1962). The rapid recovery of the subshrubs after the Morfield fire suggests that they, too, must resprout.

Crown-sprouting shrubs have a decided advantage over Utah juniper and pinyon pine during at least the first 100 years of succession because reestablishment of these trees depends entirely on seed production. The chief agents for dispersal of juniper seed are animals, as reported in a scat analysis by Arnold, Jameson, and Reid (1964). Cheek pouches of a chipmunk trapped in Mesa Verde were full of such seeds (C. L. Douglas, personal communication). The means by which pinyon seeds are spread are not as well known, but rodent caches are probably a major factor.

Woodbury (1947) stated that Utah juniper may precede pinyon pine in succession towards climax, although I found no conclusive evidence for this occurring in the Mesa Verde area. In the sample on Wetherill Mesa, pinyon was the first tree in forest establishment; but on Long Mesa, Utah juniper preceded pine by several years (Table 6). Juniper may have a small recovery advantage in that it needs no nurse plant, whereas pinyon invariably does (Phillips, 1909; Meagher, 1943; Erdman, MS.).

Shade has traditionally been considered the factor required to produce sufficiently moist conditions for

pinyon pine germination. But data collected in 1964 (Table 14) indicate that tree canopies may intercept a considerable amount of precipitation, with the result that soil moisture regimes under the litter beneath the trees are poorer than are those in the more insolated openings. Or, the lack of moisture under the canopies may be the result of depletion due to roots in that area.

TABLE 14

COMPARISON OF SOIL MOISTURE (% DRY WEIGHT) BETWEEN TREE CANOPIES AND ADJACENT OPENINGS, CHAPIN MESA*

Date	Canopy	Opening
1 May 1964	11.7	20.0
1 June 1964	8.9	11.0
1 July 1964	7.4	6.5
1 August 1964	9.5	14.3
1 September 1964	7.9	8.1

*Based on gravimetric samples from six inches below the soil surface; about four inches of litter covered the soil under the canopy.

An alternative explanation is the relatively low optimum temperature required for germination. I have found that 70°F is the optimum germinating temperature for pinyon pine seeds from Mesa Verde and this agrees with earlier studies by Kintigh (1949). Kintigh not only found that germination was most rapid and complete at this temperature, but that it was also most favorable for the growth of the seedlings. I discovered that the lethal threshold occurred between 85° and 100°F. In a recent study of the regional and local environments (Erdman, Douglas, and Marr, 1969), it was found that temperatures two inches below the ground surface in unshaded sites during summer and early fall months were commonly above 100°F, albeit for only a few hours at a time. Even at 6-inch depths, temperatures exceeded 90°.

By comparison, soil temperatures under the tree canopies were found to be moderate. Such conditions are believed to be due more to the insulating effects of tree litter than to the shade afforded by the trees themselves (Oosting, 1956).

The Status of the Present Forest Stands

The pinyon-juniper stands on Mesa Verde are approaching climax status, the condition in which no appreciable change is taking place under prevailing conditions (Hanson and Churchill, 1961). These stands have been largely free of disturbance for several centuries, yet the structure of age-classes in the pinyon population does not fit the typical structure of a climax stand. The oldest age-class, 400 to 500 years (Table 15), is younger than the age this species is capable of attaining in this environment (Smiley, 1958). Furthermore, there is a dearth of dead and fallen pinyon trees. At the same time, there

TABLE 15
AGES OF STANDS SURVEYED SUBSEQUENT TO
THE TIMBER CRUISES OF SPENCER (1964)*

Stand Location	Inside Ring Date	Age As of 1965
Ute climax, Mesa Verde Mine**	1539	426
Long Mesa climax***	1576	389
Glades climax, Chapin***	1711	254
Knife-Edge, North Rim***	1581	384
M1 station, Chapin	1529	436
M2 station, Chapin***	1647	318
CCC Camp, Chapin	1538	382
Spur, Chapin	1561	404
Research Laboratory, Chapin	1601	364
Cedar Tree Tower, Chapin	1531	434
Rock Springs, Wetherill	1457	508
Mug House, Wetherill	1606	359
South end, Wetherill	1581	384
Park-Ute boundary, Wetherill	1586	379
Double House***	1500	465
Step House	1669	296
Rock Canyon, west talus	1594	371
Rock Canyon, east talus	1644	321
Navajo Canyon, west talus	1698	267
Navajo Canyon, east talus	1723	242

*The majority of these dates are from an unpublished catalog of collections made the summer of 1961 by Thomas P. Harlan, Laboratory of Tree-Ring Research.
**Dated by James A. Erdman.
***Dated by David G. Smith.

is an abundance of old and of dead juniper trees (Erdman, MS.). I have been able to determine the age of some of the smaller juniper trees by cross-dating cores with the master tree-ring chronology for Mesa Verde. Extrapolating from these data, it is reasonable to conclude that the oldest junipers are several hundred years older than the most ancient pinyons.

These observations suggest the possibility that some factor in the environment has affected adversely the pinyon component of an otherwise relatively stable climax forest. Several possible factors such as porcupine feeding pressure, blight, and drought are discussed below.

Spencer, (1964), after making a thorough timber survey of Mesa Verde, stated that the scattered, older pinyons are from 300 to 500 years of age, indicating a relatively young pinyon element on the mesa. Dates in support of this finding are given herein (see Table 15). Spencer contended that porcupines have contributed to the maintenance of this condition, but the evidence he presents does not entirely bear out his conclusion. While feeding pressures were high in the canyons and along the perimeters of the mesa, the incidence of porcupine feeding on the mesa tops ranged from zero to only 7 percent. This can hardly account for the relatively young stands of pinyons extant on the mesa tops.

A more serious toll on pinyon pine has been exacted by the root fungus, *Leptographium*, as reported by Mielke (MS.), and by Wagener and Mielke (1961). This disease was first discovered in Mesa Verde in 1942, but field evidence indicates the infestation is of long standing. Losses of mature trees seem to have been heavy, but there are no indications that the fungus ever threatened to eliminate pinyon altogether. Wagener and Mielke observed:

Most of the escapes [sic] are small trees with limited root systems that do not come in close contact with diseased roots. These escapes provide the nucleus for a new stand on the areas over which the disease has passed. In Mesa Verde National Park all stages of residual and replacement stands of pinyon in old disease areas can be found.

Such blights also occur in many areas of the mesa beyond the park boundaries, and it may well be that these diseased stands, with a spread rate of about 40 feet each 6 years, could account for a youthful pinyon forest, especially where the incidence is highest in the deeper-soil mesa centers.

Bark beetles of the genus *Ips* are known to invade *Leptographium*-infected trees. Broods originating in such trees sometimes attack and kill neighboring pinyons, but losses from primary *Ips* attack are apparently low (Wagener and Mielke, 1961).

Pressures by porcupine and *Leptographium* may have been minor compared to the effects of wide-

spread drought the Southwest experienced several centuries ago, causing considerable die-out of the less resistant species, pinyon included (Smiley, 1958). According to Malde (1964), this drought occurred about A.D. 1600, and in the following two centuries the "forests expanded again around small stands of the older trees (those which flourished between 1300 and 1500) that had survived in sheltered habitats." Malde concluded: "It is a remarkable fact that most conifers in the Southwest are not older than 350 years, but that a few are nearly twice that age." These data resulted from research done under the Navajo Land Claim Project (Smiley, 1958). Smiley suggested that with the advent of a more moderate climate after the drought, the forests spread from the "islands" of older trees that acted as seed sources.

In a dendroclimatic study of western North America, Fritts (1965b) mapped regional variations in climate, based upon 10-year departures in tree-ring indices, which tend to support Smiley's theory. Of the period A.D. 1566-85, Fritts writes, "Dry conditions intensify in the Southwest and northern Rockies; a major drought develops until it finally extends throughout the entire West." In the Mesa Verde area, a center of low growth persisted from 1571-95. The 1600's ushered in an extremely good growth regime, for, as Fritts relates for the 1601-25 period, "An extensive, extremely moist climate expands throughout the central portions of the West." And of the period between 1641 and 1650, Fritts says, "Moist conditions intensify in the Rio Grande and Upper Colorado River Basins, expand into the southern and north-central portions of the West, but do not reach their previous maximum extent." Though the maps represent only a tentative reconstruction of otherwise undocumented climatic patterns, they do provide a plausible answer to the problem of age relations in the pinyon-juniper forests of the Mesa Verde. Utah juniper, the more xerophytic species, apparently was able to withstand the drought conditions.

A final problem in regard to climax at Mesa Verde involves the role of ponderosa pine. Getty (1935) stated, "Only rarely does yellow pine (*Pinus ponderosa*) occur in the [prehistoric] ruins, indicating that then, as now, this tree grew only in the northern and higher parts of the Mesa Verde, remote from most of the ruins." This misconception that ponderosa pine grows only along the upper reaches of the mesa seems quite prevalent. I have found pockets of this species, however, throughout the plateau in especially mesic sites, from Morfield Canyon on the east to Horse Springs and beyond in the Ute Indian Reservation; from the rimrock above The Knife-Edge at the northern escarpment to an extensive stand in the Pine Canyon area overlooking the Mancos Canyon to the south.

Some of these stands admittedly are no more than single fire- and lightning-scarred sentinels, looming above the surrounding brush and pinyon-juniper—possibly relicts of formerly more extensive stands. Yet in Bobcat Canyon on Wetherill Mesa, trees approaching 100 feet in height tower over saplings and seedlings of the same species. But in this instance the exceptional growth and probably the success of the stand are products of good ground-water supplies from local seeps and springs. Rand (1966) discussed factors related to distribution of ponderosa and pinyon pines at the Grand Canyon, Arizona. Some of the factors discussed are relevant to the Mesa Verde.

There is little indication that ponderosa pine has changed appreciably during the last millenium from its present pattern of distribution. As Getty (1935) said, ponderosa pine is rarely found in the prehistoric ruins, which predate the fourteenth century. And in the Wetherill Mesa excavations, those sites yielding some ponderosa artifacts are near the present stand of this species in Bobcat Canyon. During numerous surveys along the North Rim I found many large stumps charred from undated fires; but the trees were pinyon pine and Rocky Mountain juniper (*Juniperus scopulorum*), both common along the North Rim today.

It is true that with elevations generally above 7,000 feet and yearly precipitation averaging 18 inches, Mesa Verde should support a better stand of ponderosa pine. But because of its physiography, temperatures over most of the plateau exceed those normally expected at such an altitude. Based on the findings of Pearson (1931) and of Curtis and Lynch (1957) Parsons (MS.) attributed the status of ponderosa pine in Mesa Verde to an unfavorable temperature regime. Pearson (1950) summarized the climate of the forest interior:

The geographic range of interior ponderosa pine in the Southwest is associated with certain climatic characteristics which vary little from one locality to another. In general terms, the climate may be described as cold and dry, mean annual temperature varying from 42° to 48°F and growing season temperatures (June through September) from 58° to 65°. Maximum temperatures seldom exceed 95° and frost may occur in any month of the year. Precipitation ranges generally between 18 and 22 inches, though occasionally it may be higher or lower.

A comparison of these values with data from the weather station near park headquarters (Table 16) would suggest that Parsons' contention is valid. But similar measurements from Park Point, given in the same table, cast doubt on the temperature argument,

TABLE 16

COMPARISON OF THE MESA VERDE CLIMATIC DATA WITH SIMILAR DATA CHARACTERISTIC OF THE INTERIOR PONDEROSA PINE FORESTS OF THE SOUTHWEST

Station	Mean Temperature °F		Precipitation in inches
	Annual	June-September	
Mesa Verde, park headquarters*	50.5	68.9	18.28
Mesa Verde, Park Point**	45.4	62.5	18.84
Forest Interior***	42-48	58-65	18-22

*U.S. Weather Bureau, 1964. Data are from a Weather Bureau station at 7,070 feet elevation for the period 1923-1963.
**Erdman, Douglas, and Marr, 1969. Data are from Park Point on the North Rim at 8,575 feet elevation for the period 1962-1963.
***Pearson, 1950.

TABLE 17
COMPARISON OF TEMPERATURE AND PRECIPITATION AT MESA VERDE (PARK POINT)* AND AT PAGOSA SPRINGS, COLORADO**
RECORD PERIOD, 1962-1963

Month	Mean Temperature, °F		Precip. in inches	
	Park Point	Pagosa Springs	Park Point	Pagosa Springs
January	23.0	17.2	1.02	1.84
February	30.9	28.5	2.00	1.99
March	28.5	29.8	1.25	1.12
April	41.6	43.2	.47	.69
May	52.6	50.5	.54	.20
June	59.6	57.1	.55	.21
July	66.9	64.3	1.99	.64
August	64.1	62.6	4.79	2.70
September	59.2	57.4	1.29	2.28
October	50.7	48.5	2.82	2.56
November	37.9	35.5	1.27	1.58
December	29.8	26.1	.82	.74
Annual	45.4	43.4	18.84	16.20

*Erdman, Douglas, and Marr, 1969. Data are from a temporary weather station on the North Rim at 8,575 feet elevation.
**U.S. Weather Bureau, 1963 and 1964. Data are from a standard Weather Bureau station at 7,238 feet elevation.

for they fall well within the ranges of the ponderosa forest interior.

A comparison of weather data (U.S. Weather Bureau 1963, 1964) from Pagosa Springs, Colorado, located in the heart of a ponderosa pine climax region

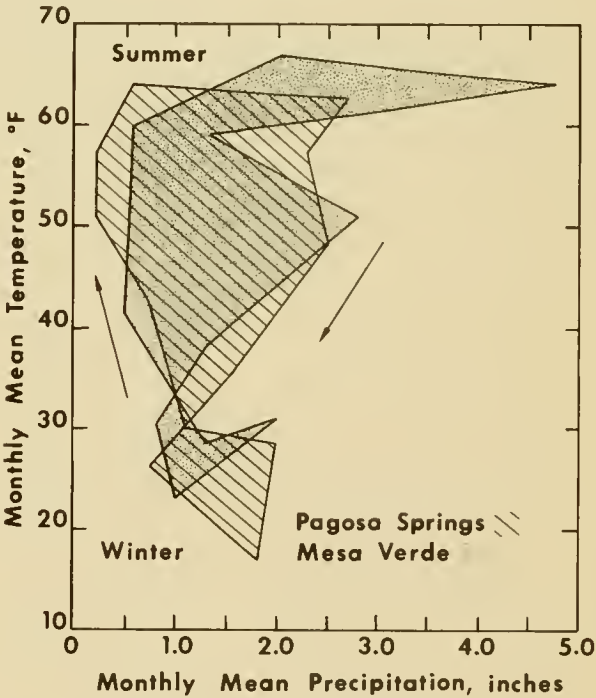


Fig. 15. Climographs comparing temperature and precipitation in the Mesa Verde (Park Point) and at Pagosa Springs, Colorado. Monthly temperature means and total precipitation have been plotted against each other and the points connected by lines. Except for the marked difference in August rainfall, the polygons are quite similar.

100 miles east of Mesa Verde, with data from Park Point (Table 17) reveals a striking similarity of monthly and annual values. Park Point is warmer but has more precipitation than Pagosa Springs. Climographs based on these data (Fig. 15) only serve to underscore the enigma concerning the scarcity of this species of pine in the Mesa Verde.

Pinon seedlings and saplings are abundant today even in stands where juniper is dominant in the older age-classes. Although Spencer (1964) asserted that pinon mortality is high during the first 100 years, I

found that seedlings, at least, survive very well. In five 1-meter quadrats established in 1962 under various microhabitats, 42 pinyon and 3 juniper seedlings were marked and their progress was followed. The latest observations in 1966 showed a loss of only four pinyon pines; the remaining seedlings appeared firmly established. In light of the greater number of pinyon seedlings than juniper seedlings and their good survival rate, some change in the present forest can be expected. It is reasonable to conclude that the percentage of pinyon tree cover will increase in the older age-classes during the next few hundred years in those stands left undisturbed.

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Many other persons have contributed significantly to the collection of the data that has culminated in this paper. In particular, I acknowledge the help of Marilyn Colyer who assisted me in the field; of Orville A. Parsons, Soil Conservation Service, Fort Collins, Colorado, who provided the soils information; of Fred E. Mang, Jr., Project photographer; and of George A. King, architect of Durango, Colorado, for drafting the base map. Dendrochronological corroboration was provided by Harold C. Fritts, Robert F. Nichols, David G. Smith, and Thomas P. Harlan, of the Laboratory of Tree-ring Research, University of Arizona, Tucson.

To my wife, Margaret Ann, I give deepest thanks for her patient encouragement through the many stages involved in the completion of this study.

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This is Contribution 49 of the Wetherill Mesa Project.

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**DISTRIBUTION OF THE
NATIVE TREES OF UTAH**

by
Kimball S. Erdman



**BIOLOGICAL SERIES—VOLUME XI, NUMBER 3
SEPTEMBER 1970**

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DISTRIBUTION OF THE NATIVE TREES OF UTAH

by
Kimball S. Erdman*

ABSTRACT

Although botanists have been actively collecting in Utah for well over a century, the distribution of many plants are as yet imperfectly known. This is, in part, due to the scattered nature of Utah herbarium material. Also the terrain of the state has impeded collection in more rugged and remote areas. The present study gathers together the data from the major collections of native Utah trees and clarifies our present understanding of tree distributions in the state. The older collection records have been exten-

sively supplemented by the field work of the author and other botanists.

The great diversity of environments due to geography, physiography, and climatic features of Utah has resulted in an interesting tree flora of fifty species and at least three naturally occurring, recognized hybrids. Although a majority of Utah's trees are mountain species, a number are strictly desert plants restricted to the Virgin or Colorado River drainages.

ACKNOWLEDGMENTS

No distribution study of this scope is completed without the assistance of many people. I am grateful to Dr. Bertrand F. Harrison and Dr. Kent H. McKnight for their counsel and advice when this project was initiated as a master's thesis. Dr. Stanley L. Welsh and Dr. Earl M. Christensen have given enthusiastic support to the continuation of this research and have added much to our present revised distribution maps. They have also been most helpful in the criticism of the manuscript. I would like to thank Dr. Albert E. Little, chief dendrologist of the United States Forest Service for his help and advice.

I am also grateful to the curators of herbaria who

assisted me: Dr. Walter P. Cottam, formerly of the University of Utah; Professor Arthur H. Holmgren of Utah State University; Mr. Stephen Clark at Weber State College; Dr. LeRoy K. Henry of the Carnegie Museum; Dr. Dan Nicholson of the U. S. National Herbarium; Dr. Charles Feddema of the U. S. Forest Service Herbarium; and to Dr. Howard S. Irwin and Dr. Patricia Kern of the New York Botanical Garden.

Finally, I would like to acknowledge the contributions of many botanists during the past hundred years. The time and effort expended in searching out the plants of Utah's rugged terrain have been monumental.

INTRODUCTION

Although botanists have been active in Utah for well over a hundred years, there is still a real need for accurate surveys and studies of plant distribution. This paper is an attempt to summarize the distribution data for all the native trees of Utah.

The earliest distribution maps of Utah tree species are those of Sudworth (1915, 1916, 1917, 1918, 1934) on the gymnosperms and Salicaceae of the Rocky Mountains. His maps were based on collections, reportings, and generalizations based on terrain. He did not show sites of specimens except on his working maps. Sudworth's maps were later revised and republished by Munns (1938). There have been a number of works since then such as Preston's *Trees of the Rocky Mountains* (1940), Harlow and Harrar's

treatment of economic trees (1958) and Fowell's work on the silvics of forest trees (1965) which included generalized maps of tree distribution. Some work on tree distribution is included in Choate's *Forests in Utah* (1965). Much more detailed maps of the genus *Pinus* were published by Critchfield and Little (1966) and Mirov (1967). Christensen published distributions of *Quercus gambelii* and on certain naturalized species, *Tamarix*, *Ulmus*, and *Elaeagnus* not covered in this paper (1949, 1950, 1955, 1962, 1963, 1964, 1965). Recently Youngberg (1966) treated the willows of Utah. Unfortunately, however, his distribution maps are not particularly informative inasmuch as they record only the presence of a species in a given county.

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There have been a number of studies of the vegetation of portions of the state both published and unpublished. Among these are Graham's study of the Uinta Basin (1937), Stanton's thesis on the ecology and floristics of the Henry Mountains (1931), Woodbury's paper (1933) on the biotic communities of Zion National Park, Burke's thesis on the plants of the Wellsville Range (1934), MacMillan's study of the floristics and ecology of the Deep Creek Mountains (1948), Preece's work on the plant communities of the Raft River Mountains (1950), Welsh's thesis on plant ecology in Dinosaur National Monument (1957), Buchanan's *Plant Ecology of Bryce Canyon National Park* (1960), Ellison's paper (1954) on the subalpine vegetation of the Wasatch Plateau, and Foster's thesis on major plant communities of the Great Basin in Utah (1966). Flowers (1959, 1960), Lindsay (1959), Hall (1960), and Woodbury and others (1958, 1959, 1960), published reports on the

plants of major reservoir sites in Flaming Gorge and Glen Canyon. Harrison, Welsh, and Moore have published on the plants of Arches National Monument (1964).

The selection of species to be included in this paper was difficult. In Utah thousands of acres are covered with pigmy forest where trees rarely reach 30 feet in height. One, therefore, is inclined to be liberal in his definition of a tree. In general, however, if a species consistently or at least commonly exceeded 10-15 feet in height, was at least two or three inches in diameter, and had a fairly well defined trunk and crown, it was included. Plants such as *Ribes aureum* and *Cornus stolonifera*, which may be this large but definitely many stemmed and shrubby, are excluded. Also, plants which are commonly shrubs and rarely reach a height of 10 or 15 feet, such as *Cowania stansburiana*, are not included.

METHODS

It has been the general practice of botanists when mapping distribution of plants to use base maps showing political subdivisions such as states and counties and a few major lakes and rivers. The size of Utah's counties and the remarkable variation of topography within them necessitates a more detailed base map. I have therefore included rivers and also major mountain ranges (See Fig. 1 and the accompanying key for the features included).

The distribution of many of Utah's trees are correlated with mountain ranges with elevations over 7,000 feet. Generally such areas will have sufficient precipitation to support a tree flora more varied than that of the pigmy forests typical of lower elevations. Only ranges with several square miles above 7,000 feet are shown on the map.

The location of species as determined from herbar-

ium specimens are indicated by dots on the maps. Certain of these specimens are cited in the species discussion. There the herbaria are listed according to their standard abbreviations: U. S. National Herbarium (US), U. S. Forest Service Herbarium (USFS), New York Botanical Gardens (NY), Carnegie Museum (CM), Utah State University (UTC), University of Utah (UT), Brigham Young University (BRY), Weber State College (no abbreviation.)

Sightings and recorded occurrences are indicated by an "X." In most cases these represent species discussed in theses or in published works, but are not validated by specimens in the herbaria consulted. Sightings represent communications from various botanists to the author. All of these sightings and recorded occurrences should eventually be verified by collections.

MOUNTAIN RANGES AND PLATEAUS (highest elevation included):

1. Raft River Mountains 9,892 ft. 2. Grouse Creek Mountains 9,042 ft. 3. Goose Creek Mountains 8,690 ft. 4. Pilot Range ca. 8,000 ft. in Utah. 5. Cedar Mountains 7,039 ft. 6. Stansbury Mountains 11,031 ft. 7. Oquirrh Mountains 10,626 ft. 8. East Tintic Mountains 8,218 ft. 9. West Tintic and Sheeprock Mountains 9,154 ft. 10. Onaqui Mountains 9,067 ft. 11. Simpson Mountains 8,450 ft. 12. Fish Springs Range 7,680 ft. 13. Deep Creek Mountains 12,101 ft. 14. Canyon Mountains 9,717 ft. 15. House Range 9,678 ft. 16. Confusion Range (southern part) 8,300 ft. 17. Needle Range 9,785 ft. 18. Wah Wah Mountains ca. 9,200 ft. 19. San Francisco Mountains 9,669 ft. 20. Mineral Mountains 9,619 ft. 21. Pine Valley Mountains 10,238 ft. 22. Beaver Dam Mountains 7,746 ft. 23. Markagunt Plateau 11,307 ft. 24. Paunsaugunt Plateau 9,630 ft. 25. Aquarius Plateau 11,328 ft. 26. Sevier Plateau 11,307 ft. 27. Tushar Mountains 12,173 ft. 28. Pavant Range 10,279 ft. 29. Wasatch Plateau 11,300 ft. 30. San Pitch Mountains 9,487 ft. 31. Wasatch Range 11,877 ft. 32. Wellsville Mountains 9,356 ft. 33. Bear River Range 9,980 ft. 34. Uinta Mountains 13,498 ft. 35. Roan Plateau (or West Tavaputs Plateau) 10,235 ft. 36. Roan Plateau (or East Tavaputs Plateau) 9,510 ft. 37. San Rafael Swell 7,921 ft. 38. La Sal Mountains 12,721 ft. 39. Abajo Mountains (or Blue Mountains) 11,360 ft. 40. Elk Ridge ca. 9,200 ft. 41. Henry Mountains 11,615 ft. 42. Kaiparowits Plateau 7,610 ft. 43. Navajo Mountain 10,388 ft.

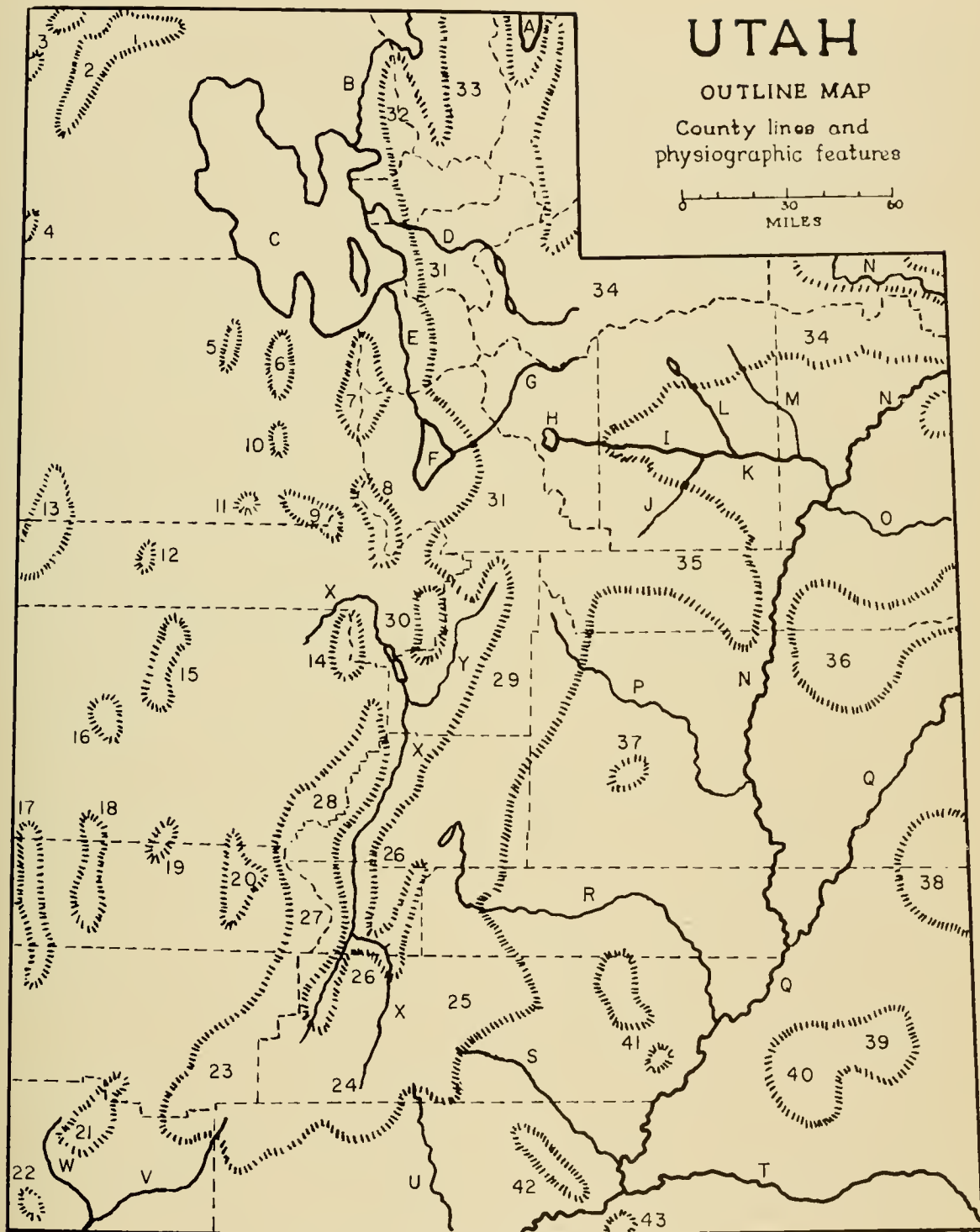


Fig. 1. Key to Map physiographic Features

RIVERS and LAKES:

A. Bear Lake B. Bear River C. Great Salt Lake D. Weber River E. Jordan River F. Utah Lake
 G. Provo River H. Strawberry Reservoir I. Strawberry River J. Indian Creek K. Duchesne River
 L. Lake Fork Creek M. Uinta River N. Green River O. White River P. San Rafael River Q. Col-
 orado River R. Dirty Devil and Fremont Rivers S. Escalante River T. San Juan River U. Paria River
 V. Virgin River W. Santa Clara River X. Sevier River Y. San Pitch River

SPECIES DISCUSSION

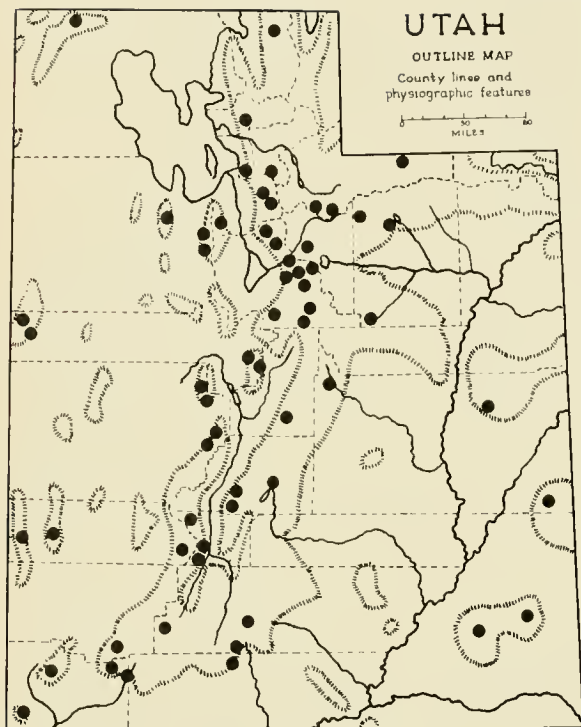


Fig. 2. *Abies concolor* (Gord. & Glend.) Lindl.

Abies concolor (Gord. & Glend.) Lindl. (Fig. 2)

White fir is one of the most widespread of Utah's conifers. It is commonly associated with Douglas-fir, blue spruce, and aspen throughout the state. With Douglas-fir it forms the very common conifer community typical of the cooler north slopes in mountain canyons from 5,000 to 9,000 feet.

White fir is conspicuously absent from Graham's (1937) treatment of the flora of the Uinta Basin. However, I found in looking over his collections at the Carnegie Museum that at least two of his collections, numbers 9641 and 9940 had been identified as *Abies lasiocarpa* but were actually *A. concolor*. There have been several additional collections in the Uinta Basin since then.

Representative Specimens: Beaver Co., Wah Wah Mts., W.P. Cottam 8080, June 10, 1940 (UT); Box Elder Co., Raft River Mts., K.S. Erdman 1537, June 8, 1965 (Weber State College); Cache Co., Logan Canyon, S. Flowers 1374, July 12, 1924 (UT); Grand Co., Roan Plateau (east), E.H. Graham 9940, July 31, 1935 (CM); Kane Co., Bryce Canyon, Buchanan 307, August 16, 1957 (UT); Piute Co., Tushar Mts., K.S. Erdman 129, May 13, 1960 (BRY); Salt Lake Co., Oquirrh Mts., J.F. Page s.n., May 13, 1965 (Weber State College); San Juan Co., Elk Ridge, K.S. Erdman 277, July 29, 1960 (BRY); Sevier Co., Gunnison, L.F. Ward 658, August 29, 1875 (US); Summit Co., China Meadows, D. Stephens s.n., July 9, 1966 (Weber State College); Tooele Co., Stansbury Range, B. Maguire 21789, June 25, 1943 (UTC); Utah Co., Hobbie Creek, B.F. Harrison 8319, May 10, 1938 (BRY); Washington Co., Beaver Dam Mts., L.S. Higgins 705, June 18, 1966 (BRY).

Abies lasiocarpa (Hook.) Nutt. (Fig. 3)

The finest and most extensive stands of subalpine fir in Utah occur in the high basins of the Uinta Mountains. This typical spireform habit of subalpine fir is a symbol of the high Uintas and other timberline areas throughout the state. From its upper altitudinal limits in southern Utah of about 11,500 feet, it descends as low as 8,000 feet on the cooler north slopes of the Raft River Mountains and other ranges of northern Utah. At higher elevations it is found most commonly with Engleman spruce and occasionally with lodgepole pine, limber pine, and aspen. Like other species which grow at high altitudes, its present known distribution reflects incomplete sampling of Utah's upper mountain slopes.

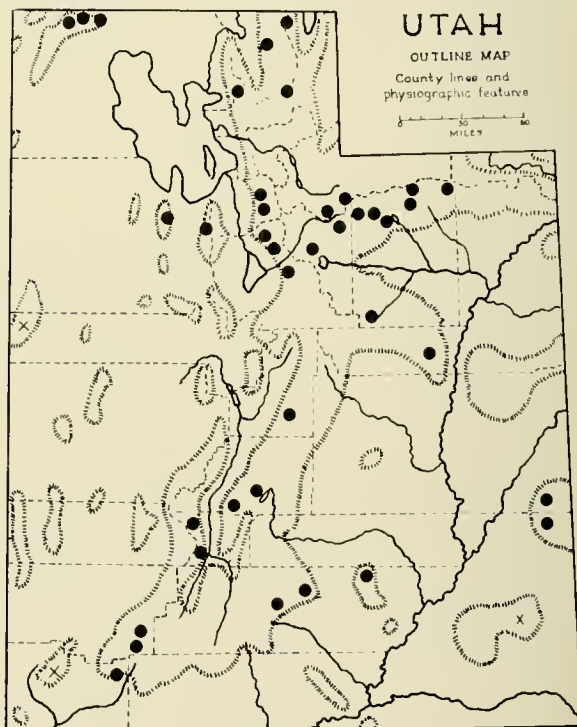


Fig. 3. *Abies lasiocarpa* (Hook.) Nutt.

Representative Specimens: Box Elder Co., Raft River Mts., K.S. Erdman 1545, June 8, 1965 (Weber State College); Cache Co., Garden City Summit, K.S. Erdman 2954, September 11, 1965 (Weber State College); Carbon Co., Roan Plateau (west), S.L. Welsh & E.M. Christensen 6542, August 10, 1967 (BRY); Duchesne Co., Uinta Mts., E.H. Graham 6633, July 3, 1931 (CM); Garfield Co., Boulder Mt., K.S. Erdman 2825, September 5, 1965 (Weber State College); Garfield Co., Henry Mts., R. McVaugh 14584, June 19-20, 1953 (NY); Grand Co., La Sal Mts., K.S. Erdman 216, July 28, 1960 (BRY); Iron Co., Cedar Breaks, S.L. Welsh & E.M. Christensen 2654, September 11, 1963 (BRY); Salt Lake Co., Lamb's Canyon, W.P. Cottam 14373, July 5, 1956 (UT); Sevier Co., Monroe Mt., K.S. Erdman 2711, September 3, 1965 (Weber State College); Summit Co., Bald Mt., K.S. Erdman 314, August 25, 1960 (BRY); Tooele Co., Stansbury Mts., E.M. Christensen s.n., July 29, 1963 (BRY).

Juniperus osteosperma (Torr.) Little (Fig. 4)

Utah juniper is probably the most widespread and

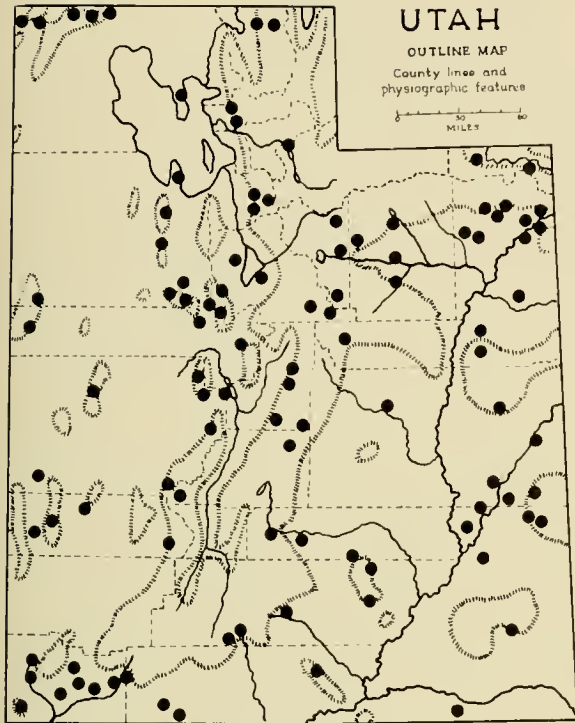


Fig. 4. *Juniperus osteosperma* (Torrey) Little

common conifer in Utah. It is the characteristic tree of lower and desert mountain slopes from 4,000 to 7,000 feet elevation, and often forms pure stands of considerable size, particularly in regions of recent invasion. Together with the two pinyon pine species in Utah it forms the pigmy forests of the desert ranges and plateaus. At higher elevations Utah juniper is associated with Gambel oak, ponderosa pine and other species.

Sargent (1922) and Preston (1940) report a closely related species, *J. monosperma*, as common throughout Utah. However, the collection records and field work do not reveal its presence in Utah.

Representative Specimens: Beaver Co., Wah Wah Mts., W.P. Cottam 8045, June 8, 1940 (UT); Box Elder Co., Raft River Mts., K.S. Erdman 1519, June 8, 1965 (Weber State College); Daggett Co., Flaming Gorge, H.C. Cutler 3445, June 21, 1940 (NY); Duchesne Co., Roan Plateau (west), E.H. Graham 9463, June 29, 1935 (CM); Garfield Co., Henry Mts., R. McVaugh 14488, June 7, 1953 (NY); Millard Co., Canyon Mts., K.S. Erdman 133, May 13, 1960 (BRY); Millard Co., House Rock Mts., J.F. Brenckle 51027, March 24, 1951 (NY); Piute Co., Marysville, P.A. Rydberg & E.C. Carlton 7008, July 21, 1905 (US); San Juan Co., Island in the Sky, G. Moore 243, July 9, 1964 (BRY); San Juan Co., Monument Valley, H.C. Cutler 3000, August 28, 1939 (NY); Summit Co., Echo, M.E. Jones s.n., May 7, 1890 (US); Tooele Co., Stansbury Island, W.P. Cottam 7607, April 13, 1940 (UT); Uintah Co., Dinosaur Nat'l. Monu., E.H. Graham 9162, June 10, 1935 (CM); Washington Co., Toquerville, O.A. Olsen 399, December 22, 1930 (USFS).

Juniperus scopulorum Sarg. (Fig. 5)

Rocky Mountain Juniper is probably second only to Utah juniper as the most widespread tree species in Utah. In view of the fact that it is found on almost every major mountain range in Utah, further work should reveal its presence in the La Sal and Pine Valley Mountains.

Although *J. scopulorum* may be a foothill species, it is common up to 9,000 feet on mountain slopes and is a characteristic tree of high rocky crags. The oldest known specimen of this species, commonly known as the Jardine Juniper, is so situated on the cliffs of Logan Canyon in northern Utah. This tree, probably the largest of its kind, is 27 feet in circumference and 44 feet in height and has been estimated to be over 3,000 years old. (Pomeroy & Dixon 1966.)

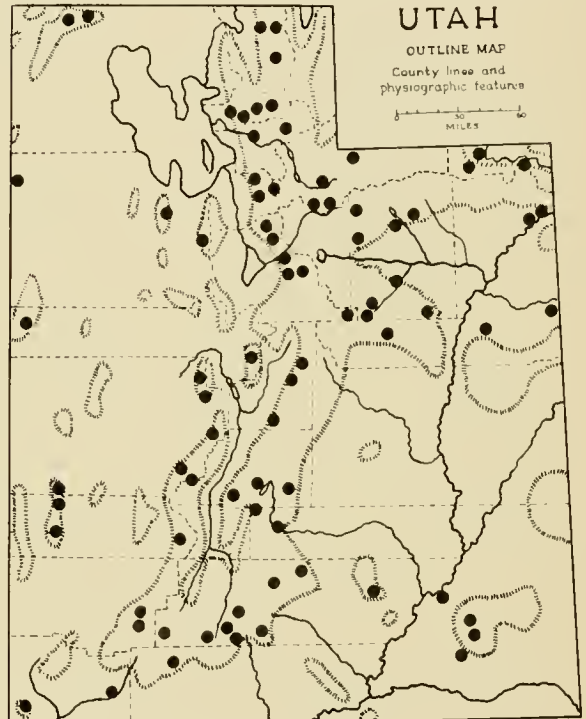


Fig. 5. *Juniperus scopulorum* Sarg.

Representative Specimens: Beaver Co., Beaver Canyon, B. Stahman 8113a, December 15, 1934 (US); Box Elder Co., Raft River Mts., K.S. Erdman 1515, June 8, 1965 (Weber State College); Daggett Co., Flaming Gorge, H.C. Cutler 3445, June 21, 1940 (NY); Duchesne Co., Roan Plateau (west), E.H. Graham 9463, June 29, 1935 (CM); Garfield Co., Henry Mts., R. McVaugh 14488, June 7, 1953 (NY); Millard Co., Canyon Mts., B.L. Robins 90, August 16, 1913 (USFS); Millard Co., Wah Wah Mts., B. Maguire & A. Holmgren 25100, May 19, 1945 (UTC); San Juan Co., Elk Ridge, Twiss s.n., July 16, 1913 (UT); San Pete Co., Six Mile Canyon, J.A. Willey 356, June 19, 1913 (USFS); Summit Co., Holiday Park, Mrs. J. Clemens s.n., August 14, 1911 (NY); Tooele Co., Stansbury Mts., E.M. Christensen s.n., July 29, 1963 (BRY); Tooele Co., Wendover, W.P. Cottam 7085, May 3, 1937 (UT); Washington Co., Beaver Dam Mts., L.C. Higgins 774, July 9, 1966 (BRY); Weber Co., Ogden Canyon, L.H. Pammel & R.E. Blackwood 3722, July 17, 1902 (US).

Picea engelmannii Parry (Fig. 6)

The high rugged summits of Utah's many mountain ranges are not very accessible. Our knowledge of the distribution of subalpine species such as Engelman spruce will remain incomplete until all such areas are carefully searched. Apparently this is a widespread species found not only in the main mountain

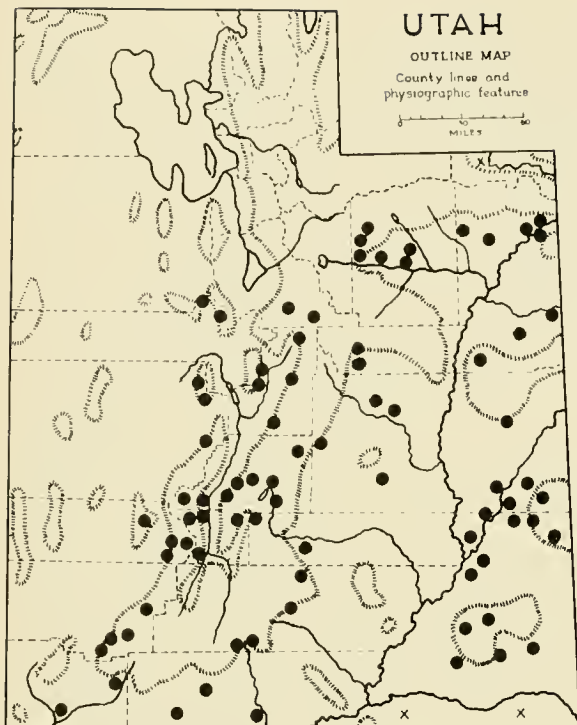


Fig. 10. *Pinus edulis* Engelm.

Representative Specimens: Beaver Co., Beaver, *S.S. Hutchings* 8444, May 2, 1938 (NY); Carbon Co., Price, *R. Hardy* s.n., May 20, 1937 (UT); Duchesne Co., Red Creek, *J. Brotherson* 480, July 20, 1965 (BRY); Emery Co., Emery, *I. Tidestrom* 1422, July 8, 1908 (US); Garfield Co., Aquarius Plateau, *Vickery* 615, May 19, 1956 (UT); Grand Co., Arches N.M., *K.S. Erdman* 188, July 26, 1960 (BRY); Kane Co., Kanab, *Knudsen* 39, December 29, 1950 (BRY); San Juan Co., Elk Ridge, *K.S. Erdman* 279, July 29, 1960 (BRY); Tooele Co., Lofgreen, *B.F. Harrison* 7236, April 15, 1934 (BRY); Uintah Co., Dinosaur Nat'l. Monu., *E.H. Graham* 9155, June 10, 1935 (CM).

Pinus flexilis James. (Fig. 11)

Limber pine is a characteristic tree of high exposed ridges, where it is often in pure stands. However, it may also be associated with *Cercocarpus ledifolius*, *Juniperus scopulorum* and other high mountain conifers. Occasionally it may occur as low as 7,500 feet. A tree near Alta in the Wasatch National Forest 28 feet in circumference and 43 feet in height is the largest known limber pine. (Communication from the U.S.F.S.)

A closely related species, *Pinus albicaulis*, has repeatedly been reported to occur in Utah (Mirov 1967, Critchfield & Little 1966, Choate 1965). However, extensive field and herbarium investigations have failed to reveal any evidence of this species occurring in Utah. Both Little and Choate (personal communication) have indicated that the claims of distribution in Utah may be based on old unverified Forest Service reports.

Representative Specimens: Box Elder Co., Pilot Mt., *W.P. Cottam* 4543, July 6, 1929 (BRY); Duchesne Co., Roan

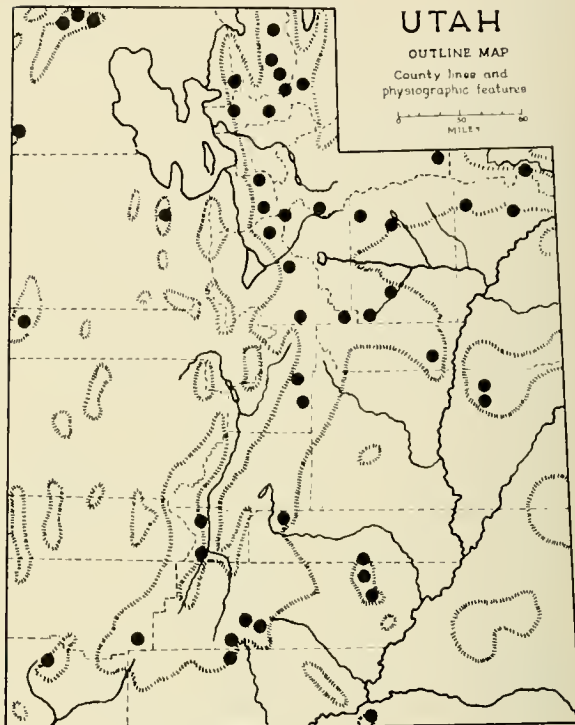


Fig. 11. *Pinus flexilis* James

Plateau (west), *K.S. Erdman* 2565, August 18, 1965 (Weber State College); Garfield Co., Bryce Canyon, *B.F. Harrison* 12039, May 10, 1953 (BRY); Garfield Co., Henry Mts., *R. McVaugh* 14478, June 7, 1953 (NY); Grand Co., Roan Plateau (east), *C. Vickery & D. Wiens* 1804, July 13-15, 1956 (UT); San Pete Co., Manti, *J. Willey* 358, June 19, 1913 (UTC); Summit Co., near Kamas, *K.S. Erdman* 300, August 25, 1960 (BRY); Tooele Co., Stansbury Mts., *E.M. Christensen* s.n., July 29, 1963 (BRY); Tooele Co., Stansbury Mts., *J.A. Harris* C20702, July 23, 1920 (CM); Uintah Co., Brush Creek, *E.H. Graham* 8271, June 23, 1933 (CM); Washington Co., Pine Valley Mts., *W.P. Cottam* 8924, June 26, 1941 (UT); Wayne Co., Thousand Lake Mt., *G.K. Gilbert* 727, July 23, 1875 (US); Weber Co., Ben Lomond Peak, *W. Call* 109, August 30, 1940 (UT).

Pinus monophylla Torr. & Frem. (Fig. 12)

Singleleaf pinyon is a common member of the pinyon forest throughout the basin and range province of Utah and Nevada. Although this species is in the canyon and East Tintic Mountains, it is inexplicably absent from the main mountain system in Utah except in the extreme northern and southern portions. Growing with *P. edulis* in southern Utah, it extends as far east as the Paria River. There are a few isolated stands in the northern Wasatch Mountains and it is reported to be present in the Crawford Range, Rich County on the Utah-Wyoming border.

Representative Specimens: Beaver Co., Wah Wah Mts., *B. Maguire* 20965, June 20, 1941 (UTC); Box Elder Co., Raft River Mts., *W.P. Cottam* 2953, June 6, 1928 (BRY); Cache Co., Blacksmith Fork, *Flowers* 17038, May 12, 1961 (BRY); Kane Co., Paria, *B.F. Harrison* 12055, May 11, 1953 (BRY); Millard Co., Canyon Mts., *K.S. Erdman* 2642, September 1, 1965 (Weber State College); Tooele Co., Deep Creek Mts., *J.A. Harris* C28613, August 5, 1928 (CM); Tooele Co., West Tintic Mts., *B. Maguire* 20730, June 15, 1941 (NY); Washington Co., Rockville, *M.E. Jones* 5220, May 15, 1894 (US).

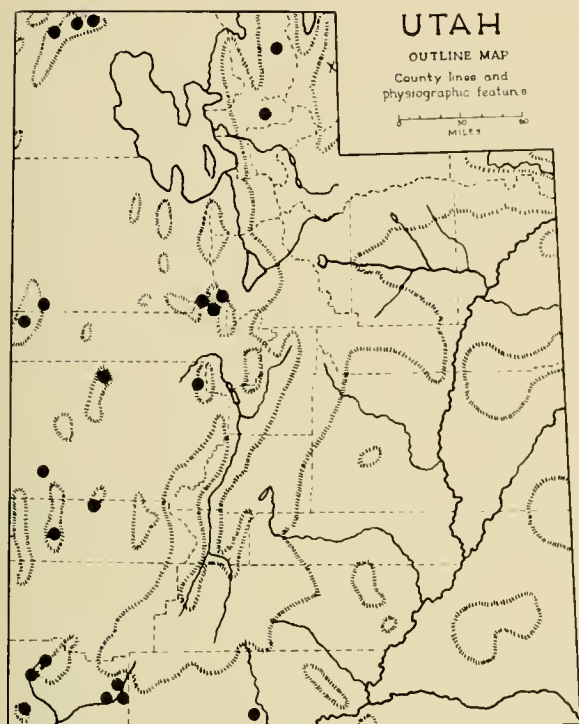


Fig. 12. *Pinus monophylla* Torr. & Frem.

Pinus ponderosa Laws. (Fig. 13)

Ponderosa pine is one of the most common conifers at elevations between 6,500 and 9,500 feet in the mountains and plateaus of southern Utah. Although occasionally occurring in open park-like stands, it is commonly associated with other species such as Gambel oak, aspen, juniper, white fir, etc. Ponderosa pine is not present in the mountains of the basin and range province of western Utah except for possibly two exceptions. It has been collected in the Wah Wah Mountains, and there is a specimen (USFS) collected in 1913 in Oak Creek Canyon, Canyon Mountains, by Bert L. Robins. This canyon is the site of a ponderosa pine plantation, but I did observe a few larger more isolated individual trees about one-fourth mile up the canyon. It is undetermined whether the older trees are natives to the canyon or remnants of earlier experimental planting.

Ponderosa pine occurs only sporadically in the Wasatch Plateau of Sevier County and only in a few sites in the Wasatch Mountains of Utah County. However, it is common at moderate elevations throughout the Uinta Basin. It has been collected on the north slope of the Uintas only in Daggett County.

Why this species is absent from the northern Wasatch Range when it grows far to the north in Idaho and Montana is a most interesting problem that reflects the general distribution of this species in the West. Ponderosa pine is common from Arizona to Canada and from the Pacific coast to the Black Hills of South Dakota and Nebraska. It is absent from the

central part of its range, namely in northern portions of Nevada and Utah and in southern regions of Idaho and Wyoming. No satisfactory answer has been found, although Baker and Korstian (1931) suggested that moisture deficiency early in the growing season might be a possible explanation.

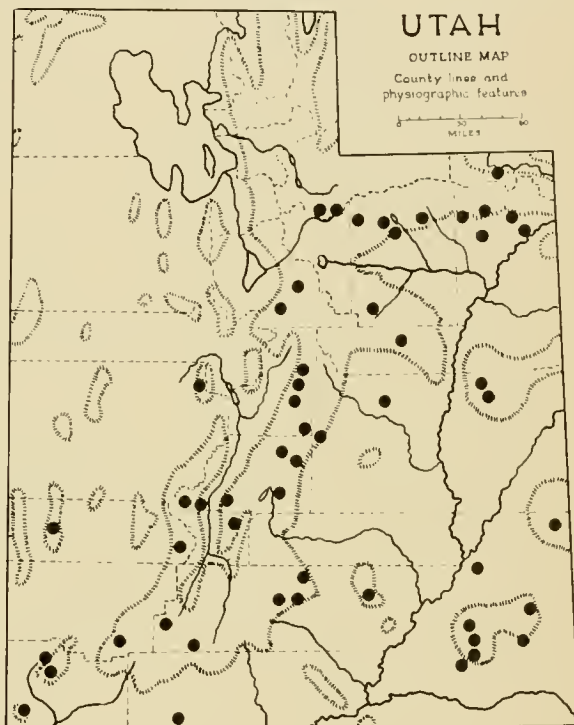


Fig. 13. *Pinus ponderosa* Laws.

Representative Specimens: Beaver Co., Wah Wah Mts., S.L. Welsh & E.M. Christensen 2687, September 13, 1963 (BRY); Daggett Co., Eagle Creek, B.F. Harrison & Larsen 7879, June 19, 1934 (BRY); Duchesne Co., Moon Lake, B.F. Harrison & Larsen 7599, May 13, 1934 (BRY); Garfield Co., Henry Mts., R. McVaugh 14479, June 7, 1953 (NY); Garfield Co., Panguitch Lake, M.E. Jones 6025, September 10, 1894 (US); Grand Co., Roan Plateau (east), E.H. Graham 9933, July 29, 1935 (CM); San Juan Co., Abajo Mts., K.S. Erdman 248, July 28, 1960 (BRY); San Juan Co., La Sal Mts., H.C. Cutler 2655, July 9, 1939 (NY); San Pete Co., Ephraim Canyon, I. Tidestrom 1144, June 11, 1908 (US); Sevier Co., Tushar Mts., K.S. Erdman 2702, September 2, 1965 (Weber State College); Utah Co., Hobbie Creek, B.F. Harrison 8319, May 10, 1938 (BRY); Washington Co., Pine Valley Mts., W.P. Cottam 6851, May 10, 1936 (UT).

Pseudotsuga menziesii (Mirb.) Franco (Fig. 14)

In nearly every mountain range in Utah over 7,000 feet in elevation there is an appropriate habitat for Douglas-fir, namely a canyon with a moist, north-facing slope. This species is almost universally present throughout Utah's mountains, and its absence from a range on the distribution map probably reflects lack of collection rather than absence of the species. Douglas-fir is adapted to a variety of habitats and may be associated with nearly all of the other conifers of the state. Although Douglas-fir is logged to

systems of Utah, such as the Wasatch and the Uintas where it is especially common, but also on isolated ranges such as the Deep Creek, La Sal, and Abajo Mountains.

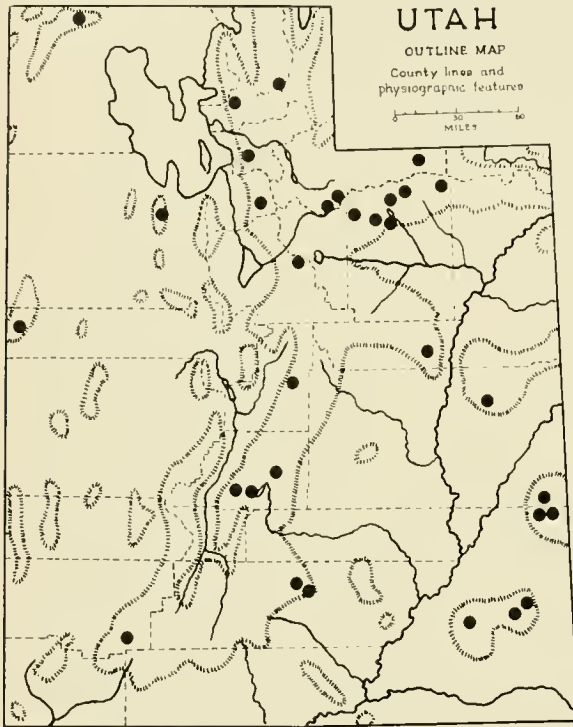


Fig. 6. *Picea engelmannii* Parry.

Representative Specimens: Box Elder Co., Raft River Mts., *W.M. Stephensen* s.n., May 18, 1965 (Weber State College); Cache Co., near Monte Cristo, *K.S. Erdman* 2600, August 28, 1965 (Weber State College); Duchesne Co., Moon Lake, *E.H. Graham* 6523, July 1, 1931 (CM); Grand Co., Roan Plateau (east), *Vickery* 1802, July 13-15, 1956 (UT); Iron Co., Cedar Breaks, *S.L. Welsh & E.M. Christensen* 2653, September 11, 1963 (BRY); San Juan Co., Abajo Mts., *P. Rydberg & A.O. Garrett* 9718, August 17-20, 1911 (NY); Sevier Co., Mt. Hilgard, *W.W. Eggleston* 10350, August 1, 1914 (US); Tooele Co., Stansbury Mts., *E.M. Christensen* s.n., July 29, 1963 (BRY).

Picea pungens Engelm. (Fig. 7)

Throughout various canyons in Utah's mountain backbone from Cedar City to the Uintas, there are small groves of spruce growing alone or in association with Douglas-fir, white fir, and aspen. The traits of symmetry and blue or silver gray cast so common in horticultural plantings, are rarely seen in mountain-grown blue spruce. Rarely is it abundant; and often, while common in one canyon, it will be absent from similar canyons just over the ridge. Its presence in the Deep Creek Mountains and on Navajo Mountain certainly indicates that deserts need not prohibit its migration. Careful searches on other isolated ranges such as the La Sal may yet reveal its occurrence.

Representative Specimens: Beaver Co., Beaver Canyon, *S.S. Hutchings* 8443, May 2, 1948 (US); Duchesne Co., Moon

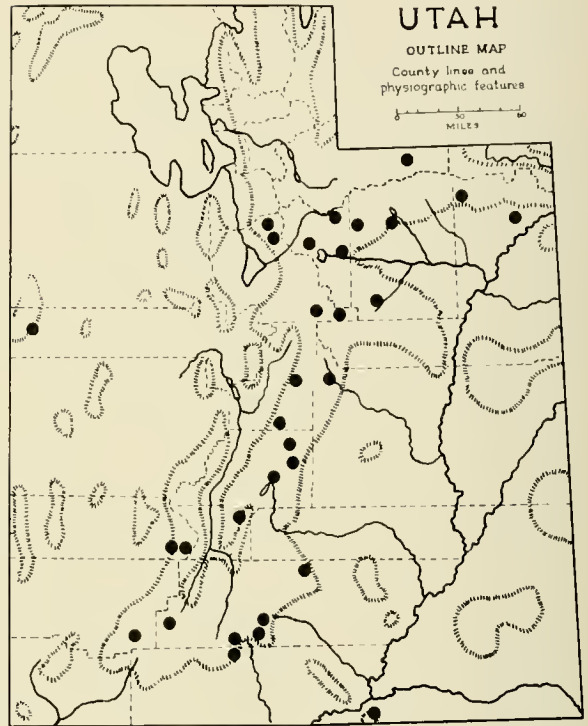


Fig. 7. *Picea pungens* Engelm.

Lake, *Harrison & Larson* 7729, June 16, 1934 (BRY); Garfield Co., Escalante Mts., *F.W. Pennell & R.L. Schaeffer* 21943, June 19, 1938 (NY); Iron Co., Cedar Creek, *S.L. Welsh & E.M. Christensen* 2616, September 11, 1963 (BRY); Piute Co., Monroe Mt., *K.S. Erdman* 2752, September 3, 1965 (Weber State College); San Pete Co., East of Mayfield, *K.S. Erdman* 2940, September 7, 1965 (Weber State College); Utah Co., Tucker, *S.L. Welsh & G. Moore* 3503, August 14, 1964 (BRY).

Pinus aristata Engelm. (Fig. 8)

Slow growing and often exceptionally long-lived, the bristlecone pine is one of the most interesting trees native to Utah. Its most characteristic habitat is on the wind swept ridges near timberline. Some individual trees in the White Mountains of California and Nevada have survived for over 4,000 years. (Ferguson 1968; Schulman 1958.)

Some of the best stands of bristlecone pine in Utah are in Cedar Breaks National Monument and in the adjoining Fishlake National Forest. Age studies during the past several years have been conducted on trees in these groves. So far the oldest tree sampled is in the Blowhard Point area of Cedar Breaks. It is estimated to be 1,630 years in age. A 1,560-year-old tree was found in Bryce Canyon National Park (personal communication, Dixie National Forest officials).

The distribution of bristlecone pine in Utah is very spotty. Its tendency to grow in high rugged mountain areas has been a hinderance to collection. Stanton (1931) described the vegetation of the Henry Mountains. His list of plants lacks a reference to bristlecone pine. However, in 1953 a botanist collected speci-

mens from a grove on the southern slopes of Mt. Hillers in the Henry Mountains. Likewise, groves have recently been discovered in the remote Roan Plateau of the Uinta Basin. As yet, the reports of bristlecone pine in the Uinta Mountains are unconfirmed. It has been found in three Great Basin ranges in Utah: Wah Wah, Needle, and Deep Creek Mountains. There are unconfirmed reports of it in the San Francisco Mountains.

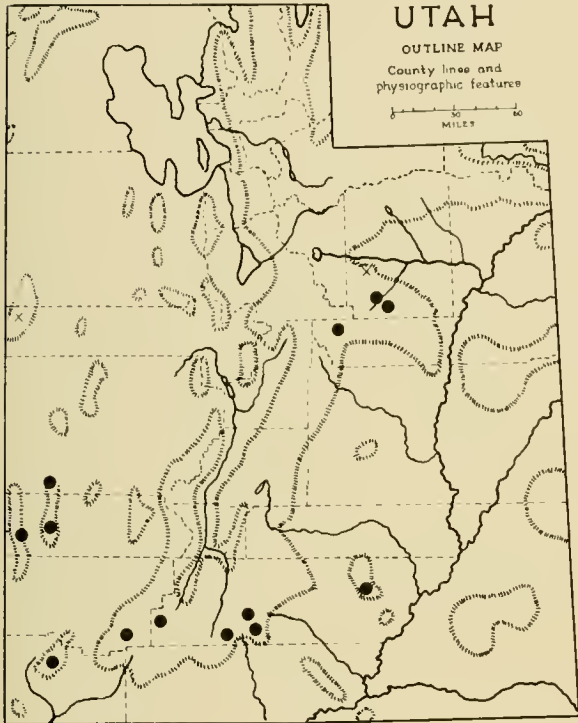


Fig. 8. *Pinus aristata* Engelm.

Representative Specimens: Beaver Co., Needle Range, *S.L. Welsh & G. Moore* 3188, July 18, 1964 (BRY); Beaver Co., Wah Wah Mts., *B. Maguire & A.H. Holmgren* 25102, May 19, 1945 (UTC); Carbon Co., Price Canyon, *S. Flowers* s.n., January 12, 1934 (UT); Duchesne Co., Roan Plateau (west), *D. Atwood* 748, September 20, 1965 (BRY); Garfield Co., Escalante Mts., *K.S. Erdman* 35, May 10, 1960 (BRY); Garfield Co., Henry Mts., *R. McVaugh* 14481, June 7, 1953 (NY); Garfield Co., Panguitch Lake, *M.E. Jones* 6003, September 7, 1894 (US); Iron Co., Cedar Breaks, *B.F. Harrison* 9864, August 24, 1940 (BRY); Washington Co., Pine Valley Mts., *F.W. Gould* 1876, July 9, 1942 (NY).

Pinus contorta Dougl. (Fig. 9)

Lodgepole pine is abundant in the Uinta Mountains where it grows from 7,000 to 10,000 feet, and in the extreme northern Wasatch or Bear River Range. Contrary to published reports, the southern most station of this species yet found in Utah is Daniels Canyon near the summit. Although Critchfield and Little in *Geographic Distribution of the Pines of the World* (1966) show this species throughout the Wasatch Plateau region south of Daniels Canyon, this is apparently based on unconfirmed reports.

Likewise the Critchfield and Little report (1966) of lodgepole pine in the Raft River Mountains of northwestern Utah appears to be in error.

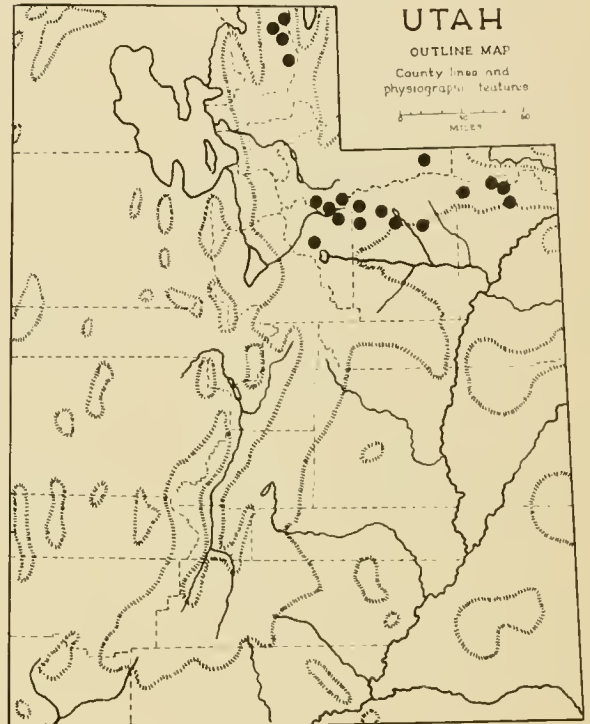


Fig. 9. *Pinus contorta* Dougl.

Representative Specimens: Cache Co., Garden City Summit, *K.S. Erdman* 2955, September 11, 1965 (Weber State College); Duchesne Co., Mt. Emmons, *B.F. Harrison & Larsen* 7744, June 16, 1934 (BRY); Summit Co., Soapstone, *K.S. Erdman* 305, August 25, 1960 (BRY); Uintah Co., Taylor Mt., *E.H. Graham* 6382, June 24, 1931 (CM); Wasatch Co., Daniels Canyon, *K.S. Erdman* 2448, August 16, 1965 (Weber State College).

Pinus edulis Engelm. (Fig. 10)

Pinyon pine is widespread and abundant on lower mountain slopes and plateaus of eastern Utah. It does not extend into the ranges of the basin and range province except in the Mineral, East Tintic, and Canyon Mountains. Although present in the Wasatch Mountains it does not occur north of Spanish Fork Canyon. Pinyon pine is common on the southern slopes of the Uintas but only in the Flaming Gorge area does it grow on the north slope.

Although the ranges of Utah's two pinyons are generally separate, there is overlap in the East Tintic Mountains and Canyon Mountains as well as in extreme southwestern Utah. In these localities there is evidence of hybridization between *Pinus edulis* and *P. monophylla* (Cole & Hiner 1963).

The largest known specimen of *Pinus edulis*, 33 feet in height and 11 feet in circumference, is in the Manti-La Sal National Forest of southeastern Utah. (Pomeroy & Dixon 1966.)

some extent, it is most important in Utah as a watershed species.

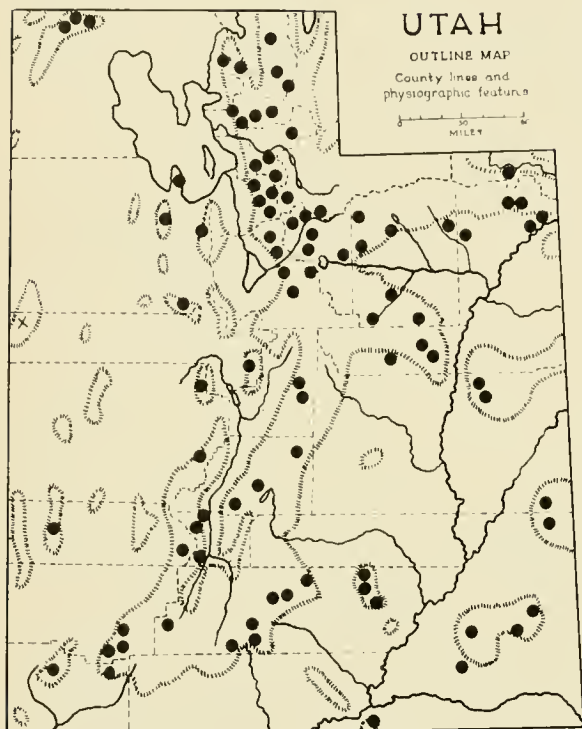


Fig. 14. *Pseudotsuga menziesii* (Mirb.) Franco

Representative Specimens: Box Elder Co., Raft River Mts., *K.S. Erdman* 1533, June 8, 1965 (Weber State College); Carbon Co., Roan Plateau (west), *E.H. Graham* 9642, July 13, 1935 (CM); Daggett Co., Flaming Gorge, *L. Williams* 494, June 2, 1932 (NY); Duchesne Co., Moon Lake, *E.H. Graham* 9386, June 25, 1935 (CM); Garfield Co., Henry Mts., *M.E. Jones* 5695bc, July 27, 1894 (US); Grand Co., La Sal Mts., *K.S. Erdman* 212, July 28, 1960 (BRY); Millard Co., Chalk Creek, *E.M. Christensen* s.n., August 3, 1966 (BRY); San Juan Co., Abajo Mts., *K.S. Erdman* 247, July 28, 1960 (BRY); San Juan Co., Navajo Mt., *H.C. Cutler* 2817, July 30, 1939 (NY); Tooele Co., Stansbury Island, *W.P. Cottam* 7606, April 13, 1940 (UT); Utah Co., Rock Canyon, *B.F. Harrison* 6181, May 12, 1933 (BRY); Washington Co., Pine Valley Mts., *L.N. Goodding* 875, May 17, 1902 (US); Weber Co., Ben Lomond Peak, *W. Call* s.n., June 28, 1940 (UT).

Acacia greggii A. Gray (Fig. 15)

The Beaver Dam Wash of Washington County, represents the northern limits of the catclaw acacia, named for its sharp spines, and is the only recorded collecting site in Utah. There is one stand near Terry's ranch which numbers about 40 individual trees.

Representative Specimen: Washington Co., Beaver Dam Wash, *S.L. Welsh* 1480, April 8, 1961 (BRY).

Acer glabrum Torr. (Fig. 16)

This maple is widespread in Utah mountains and generally grows at higher elevations than *Acer grandidentatum*. Rocky Mountain maple occurs along streams and in conifer and aspen forests.

The leaves are variable in shape and may even be palmately compound. A common fungus, almost un-

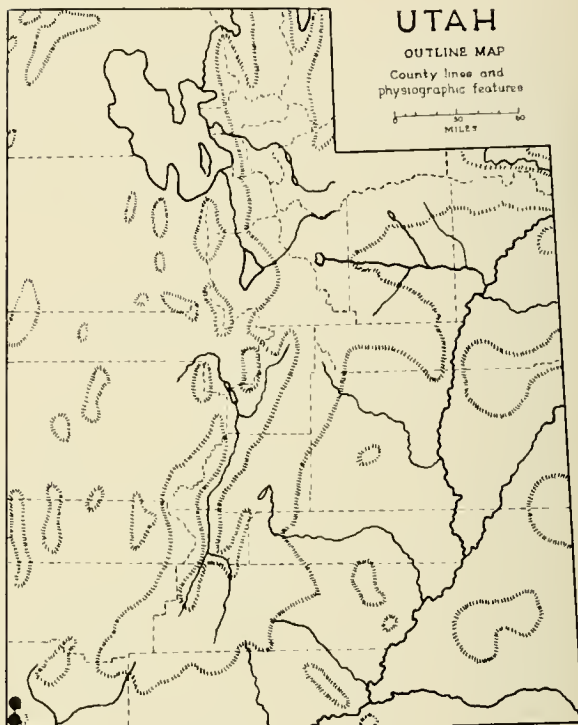


Fig. 15. *Acacia greggii* A. Gray

iversal in this area, results in striking bright red patches on the leaves.

Representative Specimens: Box Elder Co., Raft River Mts., *C. McMillan* 1504, June 18, 1948 (UT); Cache Co., Dry

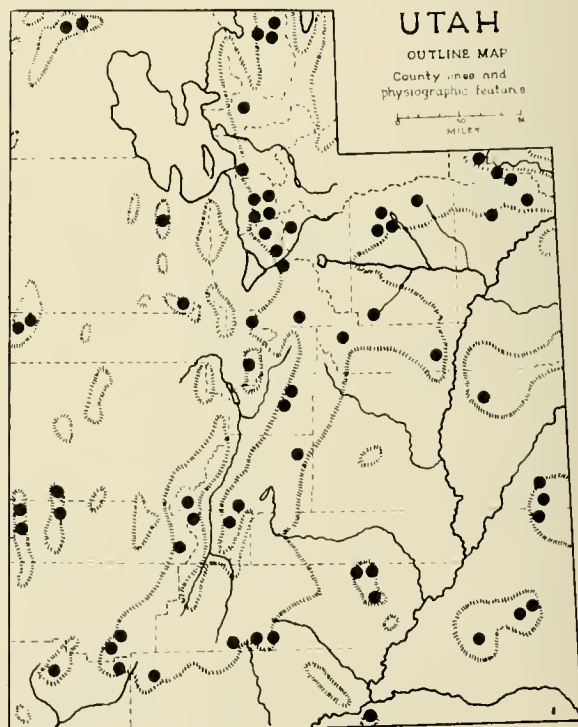


Fig. 16. *Acer glabrum* Torr.

Canyon, *B. Maguire* 13731, May 9, 1936 (NY); Carbon Co., Castlegate, *A.H. Holmgren & S. Hansen* 3508, June 29, 1944 (NY); Garfield Co., Bryce Canyon, *K.E. Weight* B-31-90, June 29, 1931 (US); Garfield Co., Henry Mts., *W.D. Stanton* 43, June 20, 1930 (UT); Grand Co., Roan Plateau (east), *E.H. Graham* 9953, August 1, 1935 (CM); Juab Co., Deep Creek Mts., *W.P. Cottam* 3202, June 16, 1928 (UT); Millard Co., Wah Wah Mts., *B. Maguire & A. H. Holmgren* 25096, May 19, 1945 (UTC); Piute Co., Box Creek, *H.J. Skidmore* 20, August 16, 1940 (USFS); Salt Lake Co., Big Cottonwood Canyon, *P.A. Rydberg* 6535, June 30, 1905 (US); San Juan Co., La Sal Mts., *P.A. Rydberg & A.O. Garrett* 8872, July 12, 1911 (NY); Tooele Co., Sheeprock Mts., *E.M. Christensen* s.n., July 28, 1963 (BRY); Uintah Co., Diamond Mt., *E.H. Graham* 8125, June 7, 1933 (CM); Washington Co., Pine Valley Mts., *F.W. Gould* 1912, July 22, 1942 (NY).

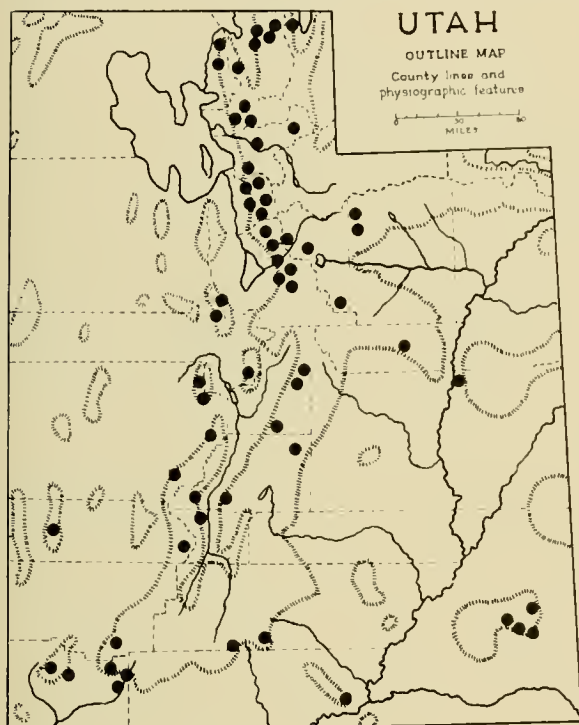


Fig. 17. *Acer grandidentatum* Nutt.

Acer grandidentatum Nutt. (Fig. 17)

The bigtooth maple is common along the north-south mountain axis in Utah and is one of the major contributors to Utah's autumn pageant. While primarily a riverbottom species associated with willows, birch, alders and aspen, it is also frequently found throughout the mountain brush zone along with oak, chokeberry, and other species. Although *A. grandidentatum* is abundant from the Wasatch Mountains south to the Pine Valley and Beaver Dam Mountains, it is uncommon in both the more eastern and western portions of the state. It has been collected in Wah Wah Canyon, East Tintic Mountains and reported to be in the Stansbury and Oquirrh Mountains in the basin and range province. Bigtooth maple has been collected numerous times in the Abajo Mountains but it has not yet been found in the La Sals or Henrys. It

has not been collected east of Rock Creek in the Uinta Mountains even though it occurs sporadically far to the east along the southern rim of the Uinta Basin.

Representative Specimens: Beaver Co., Beaver Canyon, *K.S. Erdman* 109, May 13, 1960 (BRY); Beaver Co., Wah Wah Mts., *W.P. Cottam* 8051, June 8, 1940 (UT); Cache Co., Logan Canyon, *K.S. Erdman* 2942, September 11, 1965 (Weber State College); Duchesne Co., Red Creek, *E.H. Graham* 9411, June 26, 1935 (CM); Garfield Co., Bryce Canyon, *H. Buchanan* 371, June 28, 1958 (UT); Grand Co., Desolation Canyon, *E.H. Graham* 9958, August 1, 1935 (CM); Kane Co., Kaiparowits Plateau, *J.R. Murdock* 399, May 3, 1962 (BRY); Millard Co., Canyon Mts., *K.S. Erdman* 2637, September 1, 1965 (Weber State College); Salt Lake Co., Red Butte Canyon, *A.O. Garrett* 1787, July 12, 1906 (UT); San Juan Co., Abajo Mts., *P.A. Rydberg & A.O. Garrett* 9264, July 28-29, 1911 (NY); San Pete Co., Ephraim Canyon, *I. Tidestrom* 1003, May 16, 1908 (US); Washington Co., Pine Valley Mts., *N. Gooding* 859, May 17, 1902 (US).

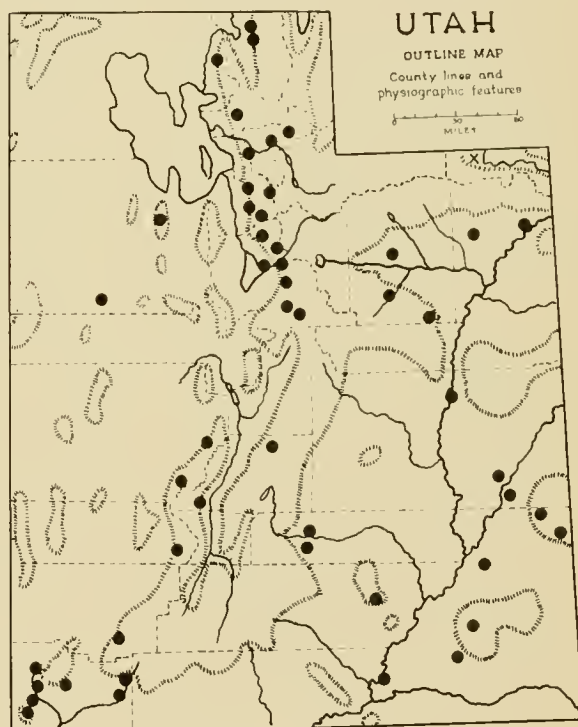


Fig. 18. *Acer negundo* L.

Acer negundo L. (Fig. 18)

Well adapted to a variety of climates, box elder is widely distributed throughout the United States. In Utah it is restricted to streamsidess and washes where it is often one of the most common trees. Box elder's distribution in Utah is spotty and may reflect in part an extension of its range due to its frequent use as an ornamental tree.

Representative Specimens: Beaver Co., Beaver Canyon, *I. Tidestrom* 2872, September 2, 1909 (US); Duchesne Co., Roan Plateau (west), *S.L. Welsh & E.M. Christensen* 6618, August 12, 1967 (BRY); Garfield Co., Henry Mts., *R. McVaugh* 14490, June 7, 1953 (NY); Salt Lake Co., Lamb's Canyon, *Vickery* 1505, October 8, 1957 (UT); San Juan Co., La Sal Mts., *H.C. Cutler* 2643, (NY); San Juan Co., Natural Bridges Nat'l. Monu., *S.L. Welsh & G. Moore* 3587, August

15, 1964 (BRY); Sevier Co., Salina Canyon, *K.S. Erdman* 2919, September 7, 1965 (Weber State College); Tooele Co., Dugway Range, *J.A. Harris* C28624, August 6, 1928 (CM); Uintah Co., Dinosaur Nat'l. Monu., *E.H. Graham* 7724, May 18, 1933 (CM); Utah Co., Thistle, *K.S. Erdman* 2589, August 18, 1965 (Weber State College); Washington Co., Beaver Dam Mts., *L.C. Higgins* 688, May 27, 1966 (BRY); Weber Co., Ogden Canyon, *A.E. Hitchcock* 1499, August 19, 1913 (US).

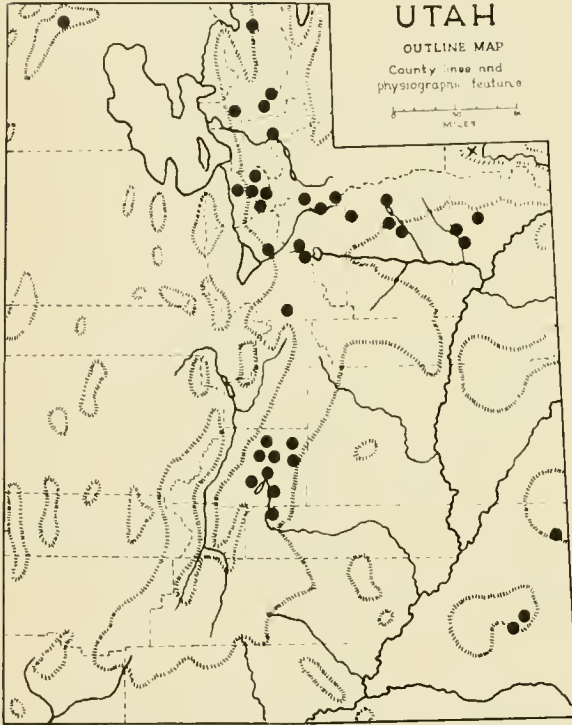


Fig. 19. *Alnus tenuifolia* Nutt.

Alnus tenuifolia Nutt. (Fig. 19)

Thin-leaf alder forms large shrubby thickets in high mountain regions, although it is more common along streams at lower elevations. It is like bristlecone pine and blue spruce in that it has a very spotty distribution. While very abundant in one canyon, it may be absent from drainages on either side. For example, alder is very common in the drainages of the Fremont River and Salina Creek, but is absent from Twelve-mile Creek ten miles to the north. It has been found at only one site along the Wasatch Plateau but is common in certain canyons of the Wasatch and Uinta Mountains. It is present in only three of the isolated ranges of the state, the Raft River, La Sal and Abajo Mountains.

Representative Specimens: Box Elder Co., Raft River Mts., *Preece* 775, June 29, 1947 (UT); Salt Lake Co., Red Butte Canyon, *S.G. Stokes* s.n., May 15, 1900 (US); San Juan Co., Abajo Mts., *P.A. Rydberg & A.O. Garrett* 9252, July 28-29, 1911 (NY); Sevier Co., Salina Canyon, *K.S. Erdman* 2918, September 7, 1965 (Weber State College); Uintah Co., Ashley Creek, *E.H. Graham* 6259, June 23, 1931 (CM); Wasatch Co., Strawberry Reservoir, *R.H. Foster* 268, October 13, 1964 (BRY); Wayne Co., Fremont River, *K.S. Erdman* 2807, September 4, 1965 (Weber State College).

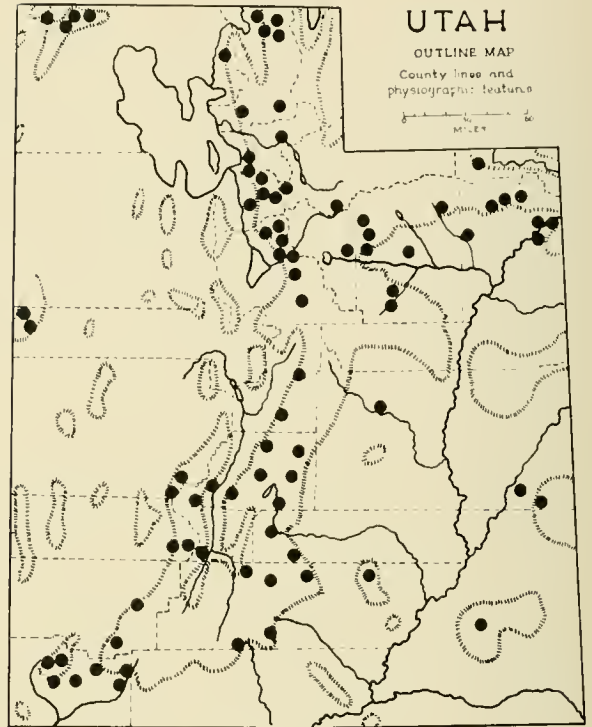


Fig. 20. *Betula occidentalis* Hook.

Betula occidentalis Hook. (Fig. 20)

River birch is common throughout the state and is usually found near running water, springs, and seeps. In the basin and range province, it has been collected only in the Deep Creek Mountains.

Representative Specimens: Box Elder Co., Raft River Mts., *Porter* 75, July 2, 1949 (UT); Davis Co., Bountiful, *Mrs. J. Clemens* s.n., September 22, 1909 (NY); Duchesne Co., Roan Plateau (west), *K.S. Erdman* 2517, August 17, 1965 (Weber State College); Garfield Co., Bryce Canyon, *K.E. Weight* G-31-114, July 10, 1931 (US); Grand Co., La Sal Mts., *K.S. Erdman* 227, July 28, 1960 (BRY); Iron Co., Parowan, *W.W. Eggleston* 14902, September 17, 1918 (US); Millard Co., Pavant Mts., *Mrs. F.M. Stone* 223, May 9, 1934 (NY); San Juan Co., Elk Ridge, *P.A. Rydberg & A.O. Garrett* 9321, July 31, 1911 (NY); San Pete Co., Ephraim Canyon, *Jorgensen* 42, August 5, 1950 (UT); Uintah Co., Dinosaur Nat'l. Monu., *E.H. Graham* 7542, April 28, 1933 (CM); Utah Co., Provo Canyon, *S.L. Welsh* 3813, October 20, 1964 (BRY).

Celtis reticulata Torr. (Fig. 21)

In Utah the netleaf hackberry is very often overlooked. Indeed, there is little to make this tree attractive. Its gnarled and twisted branches, often infected with a fungus causing a witches broom effect, bear leaves equally deformed by insect galls.

The distributional pattern of this tree type in Utah is certainly distinctive. Generally it is a tree of the Colorado River and Virgin River drainages, but it is found in a few other isolated areas. Its presence in the Uinta Basin along the Green River can be explained by its migration up that stream valley. However, it is quite common on the foothills of the Wasatch Moun-

tains and on low mountain ranges immediately around the Great Salt Lake, such as Stansbury Island and Promontory Mountains. Since the fruit is commonly eaten by birds, its presence in the Great Salt Lake-Utah Lake area might be due to migratory patterns of bird flight.

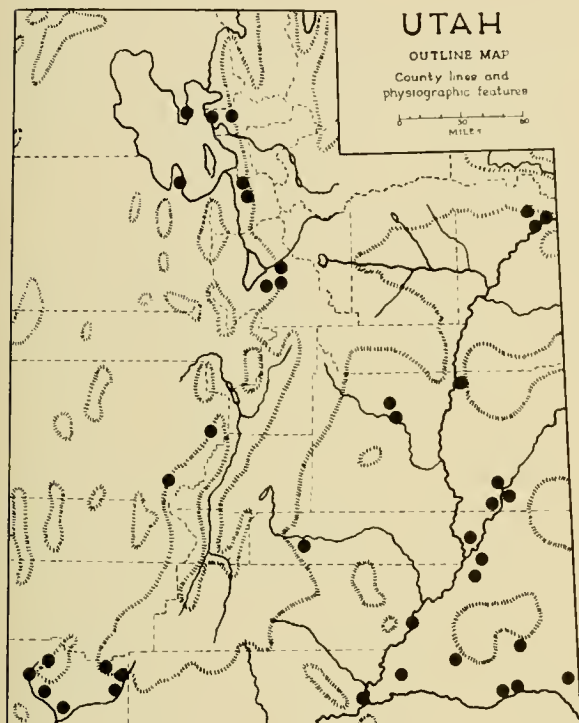


Fig. 21. *Celtis reticulata* Torr.

Representative Specimens: Box Elder Co., East Promontory Point, *S. Flowers* 1037, August 8, 1929 (UT); Grand Co., Desolation Canyon, *E.H. Graham* 9967, August 2, 1933 (CM); Kane Co., Hole-in-the-rock, *B.F. Harrison* 12108, May 14, 1935 (BRY); Millard Co., Fillmore, *K.S. Erdman* 2674, September 2, 1965 (Weber State College); Salt Lake Co., Beek's Hot Springs, *A.O. Garrett* 6881, May 18, 1935 (UT); San Juan Co., Canyonlands Nat'l. Park, *G. Moore* 368, May 15, 1965 (BRY); San Juan Co., Hovenweep Nat'l. Monu., *A.P. Plummer* 355, June 4, 1950 (USFS); Uintah Co., Dinosaur Nat'l. Monu., *E.H. Graham* 7723, May 18, 1933 (CM); Washington Co., Zion Nat'l. Park, *Mrs. F.M. Stone* 175, May 7, 1934 (NY); Wayne Co., Capital Reef N.M., *R. McVaugh* 14517, June 9, 1953 (NY).

Cercis occidentalis Torr. (Fig. 22)

The Judas tree or redbud, is one of the showiest trees of Utah. Bright clusters of small magenta flowers are scattered all along the twigs. It is restricted in Utah to Washington County and to the southern portion of the Colorado Gorge. Many of the latter sites have been covered by the waters of Lake Powell behind the Glen Canyon Dam. Most likely, however, this species is still present in some of the higher tributary canyons.

Representative Specimens: San Juan Co., Aztec Creek, *Lindsay* 147, July 25, 1958 (UT); Washington Co., Gunlock, *L.K. Shumway* 35, April 9, 1961 (BRY).

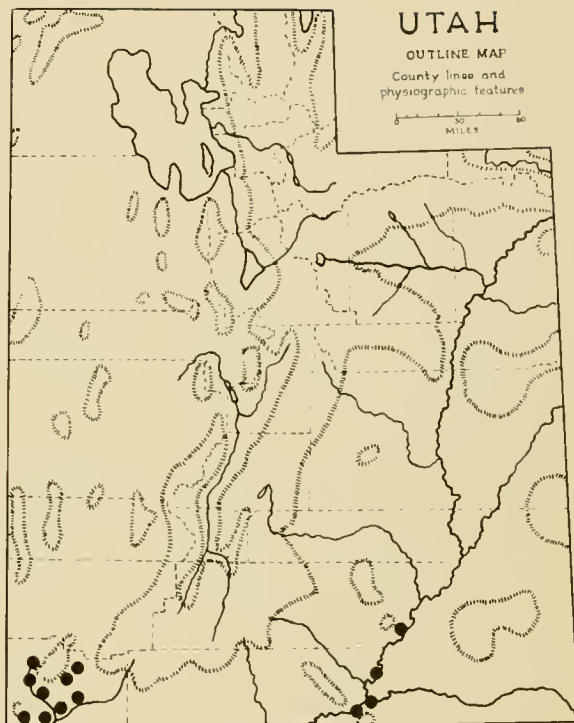


Fig. 22. *Cercis occidentalis* Torr.

Cercocarpus ledifolius Nutt. (Fig. 23)

Growing from about 5,000 feet up to 9,000 feet, the curl leaf mountain mahogany is a common species of the mountain brush zone and upper pigmy forest.

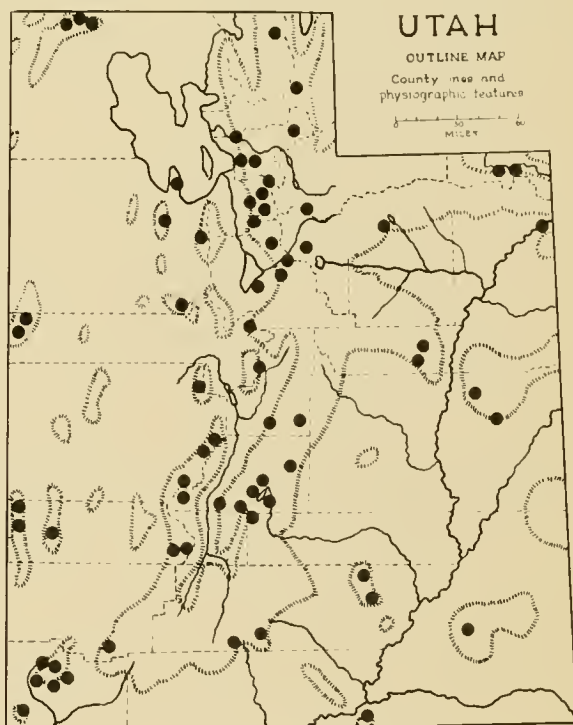


Fig. 23. *Cercocarpus ledifolius* Nutt.

It thrives on bare rocky outcrops where few other species grow. In these situations it is commonly associated with Rocky Mountain juniper and limber pine.

Occasionally *C. ledifolius* is found with *C. montanus* and there is considerable evidence of hybridization. I have seen plants in such mixed communities showing all degrees of leaf shape from the narrow revolute leaves of *C. ledifolius* to the broad, serrate leaves of *C. montanus*. Further work is needed to verify the suspected hybrid origins of such plants.

Representative Specimens: Beaver Co., Canyon, *I. Tidestrom* 2876, September 2, 1909 (US); Box Elder Co., Raft River Mts., *Preece* 1017, May 26, 1949 (UT); Cache Co., Logan Canyon, *K.S. Erdman* 2947, September 11, 1965 (Weber State College); Carbon Co., Roan Plateau (west), *E.H. Graham* 9634, July 14, 1935 (CM); Daggett Co., Red Canyon, *L. Williams* 591, June 10, 1932 (UTC); Garfield Co., Henry Mts., *R. McVaugh* 14641, June 19-20, 1953 (NY); Juab Co., Deep Creek Range, *A.H. Holmgren*, August 9, 1944 (UTC); Millard Co., Canyon Mts., *K.S. Erdman* 131, May 13, 1960 (BRY); Salt Lake Co., Mt. Olympus, *S. Flowers* 458, April 15, 1925 (UT); San Juan Co., Elk Ridge, *S. Flowers* 61, August 4, 1954 (UT); San Juan Co., Navajo Mt., *A.H. Holmgren & B.C. Maguire* 10664, July 6, 1954 (NY); Sevier Co., Fish Lake, *L.F. Ward* 38, May 14, 1875 (US); Washington Co., Pine Valley, *W.P. Cottam* 1178, August 26, 1927 (BRY).

Cercocarpus montanus Raf. (Fig. 24)

Alder-leaf mountain mahogany seldom reaches tree size. This may be related to extensive use by browsing animals. It is more tolerant of desert conditions than *C. ledifolius* and is common in the pinyon-juniper forests and mountain brush zones. It is absent in most of the basin and range province but very widespread elsewhere in the state.

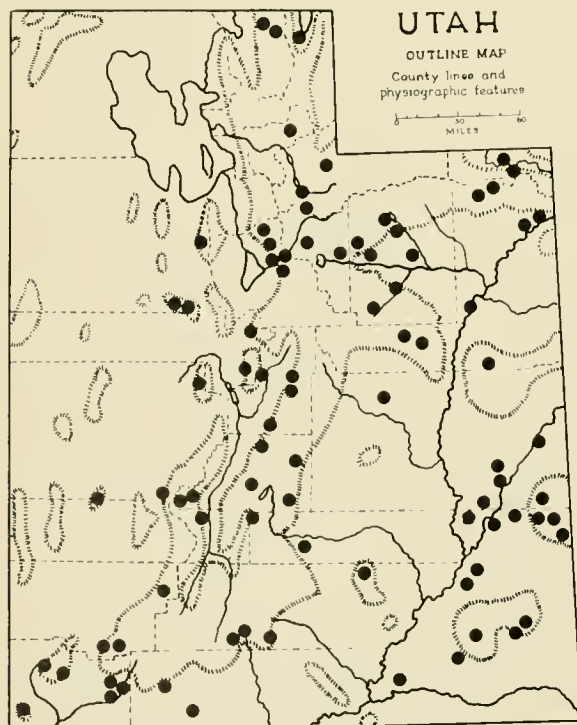


Fig. 24. *Cercocarpus montanus* Raf.

Representative Specimens: Beaver Co., Frisco, *M.E. Jones* 1822, June 25, 1880 (US); Cache Co., Logan Canyon, *A.H. Holmgren* 3565, July 15, 1944 (NY); Duchesne Co., Moon Lake, *E.H. Graham* 9387 & 9389, June 25, 1935 (CM); Garfield Co., Bryce Canyon Nat'l. Park, *H. Buchanan* 201, July 15, 1957 (UT); Garfield Co., Henry Mts., *R. McVaugh* 14685, June 10-20, 1953 (NY); Grand Co., Abajo Mts., *K.S. Erdman* 270, July 29, 1960 (BRY); San Juan Co., south of Moab, *A.H. Holmgren & S. Hansen* 3323, June 15, 1944 (UTC); San Pete Co., Ephraim Creek, *A.H. Holmgren & R. Shaw* 7682, June 13, 1948 (NY); Sevier Co., Salina Canyon, *M.E. Jones* 5441m, June 15, 1894 (US); Tooele Co., Sheeprock Mts., *E.N. Christensen* s.n., July 28, 1963 (BRY); Uintah Co., Roan Plateau (east), *Vickery* 1738, July 13-15, 1956 (UT); Utah Co., Provo Canyon, *S.L. Welsh & G. Moore* 6362, July 16, 1967 (BRY); Washington Co., Silver Reef, *M.E. Jones* 5163L, May 4, 1894 (US).

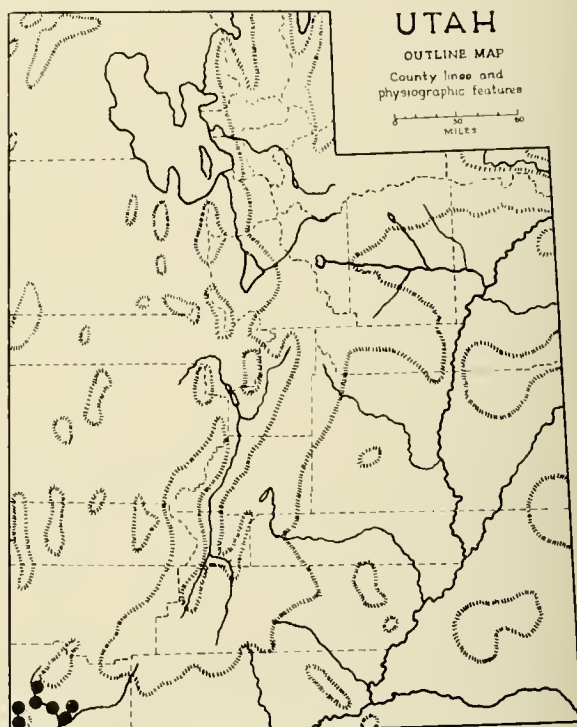


Fig. 25. *Chilopsis linearis* (Cav.) Sweet

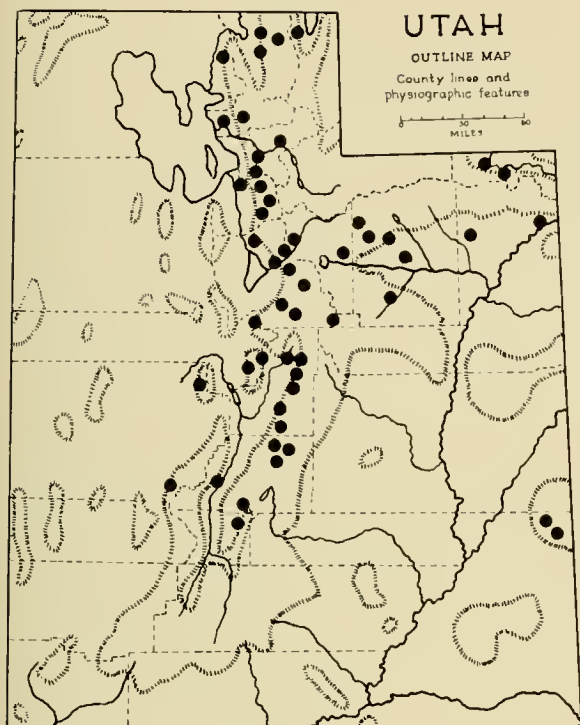
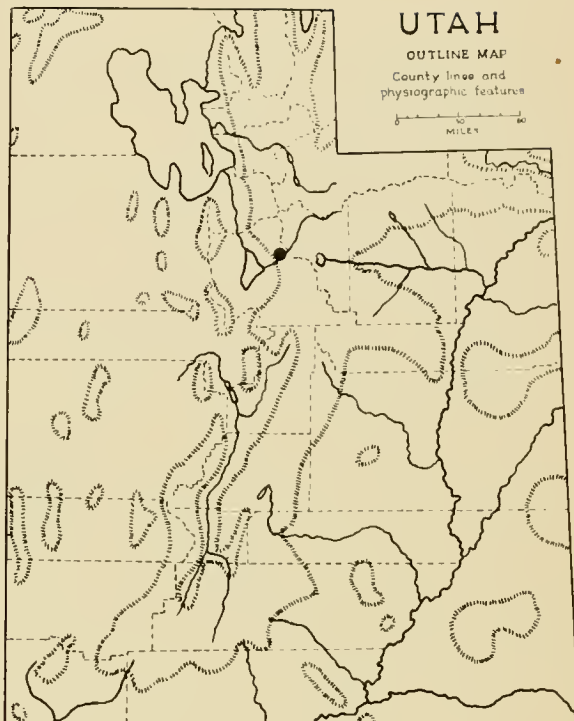
Chilopsis linearis (Cav.) Sweet (Fig. 25)

The desert willow has elongated graceful leaves and showy flowers and is one of the loveliest trees of southern Utah. It is found only in Washington County where it grows along streams or on moist hill-sides. However, it has been grown as an ornamental tree in Utah as far north as Ogden, where I observed it flourishing in an experimental garden.

Representative Specimens: Washington Co., Beaver Dam Wash, *K.S. Erdman* 72, May 11, 1960 (BRY); Washington Co., Santa Clara, *W.P. Cottam* 1182, August 28, 1927 (BRY).

Crataegus rivularis Nutt. (Fig. 26)

Utah's common hawthorne is generally restricted to streamsides primarily of the Wasatch and Uinta Mountains. It is common in the central plateau section of the state as far south as Piute County. There are a few scattered records elsewhere but it appears to be absent almost entirely from the basin

Fig. 26. *Crataegus rivularis* Nutt.Fig. 27. *Crataegus succulenta* Schrad.

and range province of western Utah and uncommon in the isolated ranges of southeastern Utah.

Representative Specimens: Box Elder Co., Corinne, A. Wetmore 347, July 1, 1915 (US); Daggett Co., Sheep Creek, L. Williams 521, June 3, 1932 (UTC); Duchesne Co., Red Creek, E.H. Graham 9448, June 27, 1935 (CM); Duchesne Co., Roan Plateau (west), J.A. Willey 24, May 23, 1918 (USFS); Millard Co., Canyon Mts., B.L. Robins 105, August 16, 1913 (USFS); Piute Co., Monroe Mt., K.S. Erdman 2762, September 3, 1965 (Weber State College); San Juan Co., La Sal Mts., W.P. Cottam 2288, June 16, 1927 (BRY); San Pete Co., Ephraim Canyon, W.W. Eggleston 10113, May 20-26, 1914 (US); Uintah Co., Dinosaur Nat'l. Monu., A.H. Holmgren & N.H. Holmgren 14245, June 29, 1962 (NY); Utah Co., Provo, K.S. Erdman 334, July, 1959 (BRY).

Crataegus succulenta Schrad. (Fig. 27)

This hawthorne is widespread from New England to Colorado and Arizona, but the only record in Utah is from along the Provo River where it cuts through the Wasatch Mountains.

Representative Specimens: Utah Co., Provo Canyon, A.O. Garrett 8439, May 20, 1942 (UT); Utah Co., Provo Canyon, S.L. Welsh 1882, October 2, 1962 (BRY).

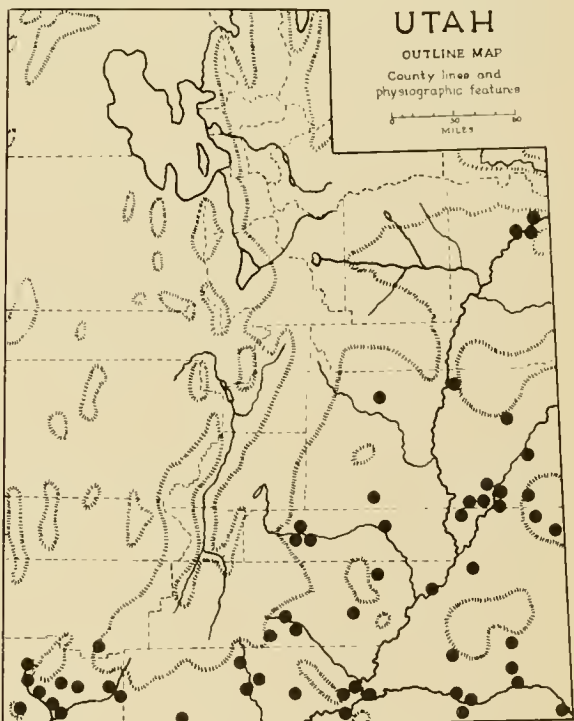
Fraxinus anomala Torr. (Fig. 28)

Unlike other species of the genus *Fraxinus* which have compound leaves, *F. anomala* usually has simple leaves. Occasionally, however, one can find single-leaf ash with at least a few compound leaves which is more typical of the genus.

The single-leaf ash grows throughout Utah's Colorado plateau region where it may be a common member of the pinyon-juniper forest. Apparently it has migrated up along the Green River into the Uinta

Basin, its northern most site in Utah. Its only Great Basin location in Utah is just over the divide north of Washington County.

Representative Specimens: Emery Co., Buckhorn Mts., B.F. Harrison 8081, May 8, 1936 (BRY); Garfield Co.,

Fig. 28. *Fraxinus anomala* Torr.

Escalante, *W.P. Cottam* 4401, June 19, 1929 (UT); Grand Co., Desolation Canyon, *E.H. Graham* 9968, August 2, 1935 (CM); Grand Co., Moab, *K.S. Erdman* 192, July 27, 1960 (BRY); Iron Co., Cedar Creek, *W.P. Cottam* 6742, May 9, 1936 (UT); San Juan Co., Bluff, *A.H. Holmgren*, 3154, May 9, 1944 (US); San Juan Co., Bridge Canyon, *A.H. Holmgren* & *J.M. Goddard* 9946, May 6, 1954 (NY); Uintah Co., Dinosaur Nat'l. Monu., *E.H. Graham* 7687, May 17, 1933 (CM); Washington Co., St. George, *L.N. Gooding* 779, May 13, 1902 (US); Wayne Co., Capitol Reef Nat'l. Monu., *A. Carter* 1553, May 25, 1940 (NY).

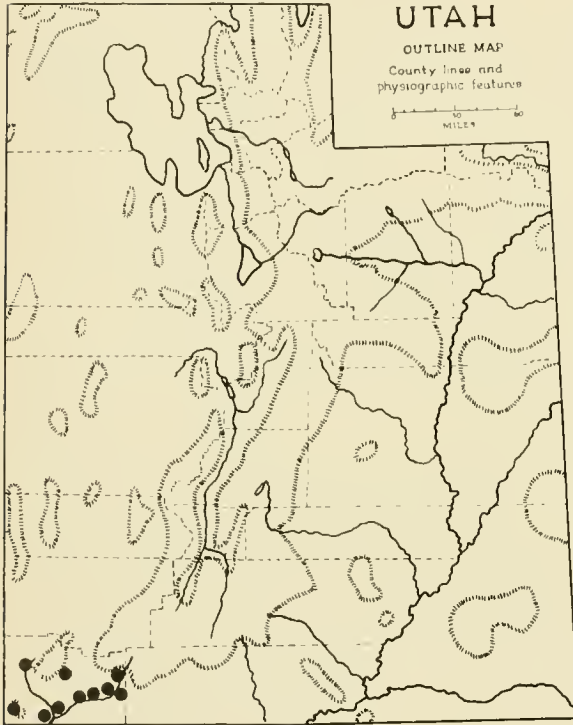


Fig. 29. *Fraxinus velutina* Torr.

Fraxinus velutina Torr. (Fig. 29)

The velvet ash, named for the vestiture of the undersurface of the leaves is a common tree shading the banks of the Virgin River and its tributaries. This species is restricted to Washington County.

Representative Specimens: Washington Co., Beaver Dam Mts., *L.C. Higgins* 425, April 9, 1966 (BRY); Washington Co., Hurricane, *W.W. Eggleston* 14858, September 14-15, 1918 (US).

Ostrya knowltonii Cov. (Fig. 30)

Knowlton's hophornbeam is a slender tree found in moist canyons throughout the southwest desert. Nowhere in Utah is it common or abundant, except in draws and more moist slopes in the Needles area of Canyonlands National Park. Utah records that all habitation of this type of tree is in the Colorado drainage south of Moab. Undoubtedly much of its habitat was destroyed with the flooding of Glen Canyon.

Representative Specimens: Grand Co., Moab, *W.P. Cottam* 2145, June 8, 1927 (UT); San Juan Co., Canyonlands Nat'l. Park, *G. Moore* 336, May 14, 1965 (BRY).

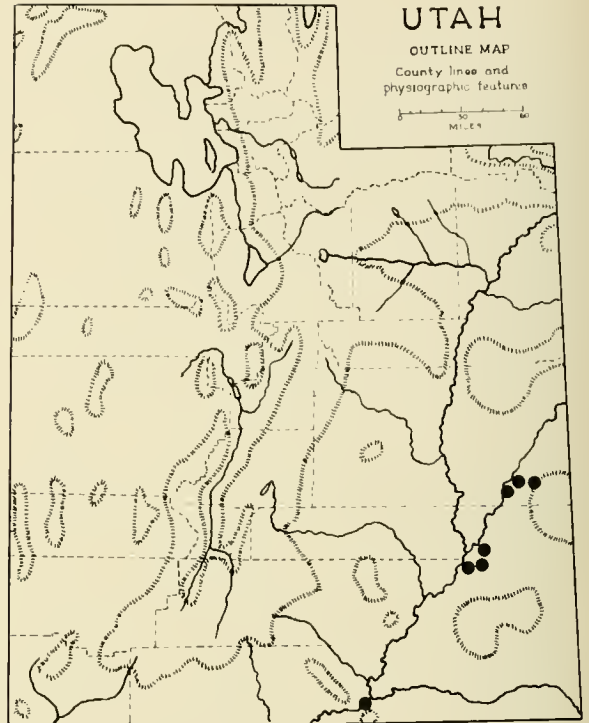


Fig. 30. *Ostrya knowltonii* Cov.

Populus angustifolia James (Fig. 31)

Narrow-leaf cottonwood occurs in mountainous regions from Mexico northward into Canada. In Utah it is generally restricted to canyons and washes from

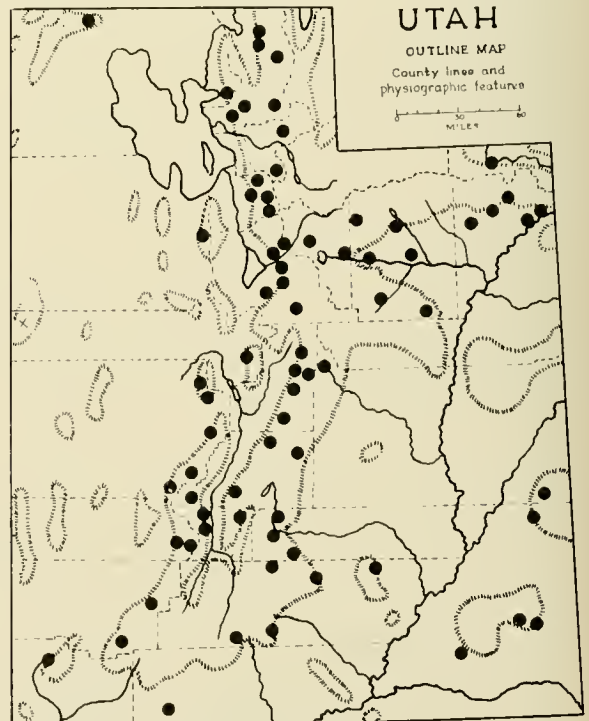


Fig. 31. *Populus angustifolia* James

3,000 to 8,000 feet. The tree may grow in pure groves or in mixed river-bottom forests with maples, willows, alders, birch, etc. Although there are unverified reports from a number of ranges from western Utah, the only collection records are from the Canyon and Oquirrh Mountains.

Representative Specimens: Box Elder Co., Raft River Mts., *W.P. Cottam* 2955, June 5, 1928 (BRY); Duchesne Co., Moon Lake, *K.S. Erdman* 2491, August 17, 1965 (Weber State College); Garfield Co., Bryce Canyon, *K.E. Weight* B-31-148, August 15, 1931, (US); Grand Co., La Sal Mts., *K.S. Erdman* 204, July 27, 1960 (BRY); Millard Co., Canyon Mts., *J.A. Harris* C28384, July 21, 1928 (CM); Millard Co., Pavant Mts., *Mrs. F.M. Stone* 226, May 9, 1934 (NY); Piute Co., Box Creek, *D.G. Harrington* 14, July 31, 1940 (USFS); San Juan Co., Abajo Mts., *K.S. Erdman* 261, July 29, 1960 (BRY); Uintah Co., Dinosaur Nat'l. Monu., *S.L. Welsh* 67, April 30, 1955 (BRY); Utah Co., Thistle, *I. Tidestrom* 94, August 8, 1907 (US); Washington Co., Pine Valley Mts., *W.P. Cottam* 8964, June 27, 1941 (UT); Weber Co., abv. Huntsville, *K.S. Erdman* 2593, August, 1965 (Weber State College).

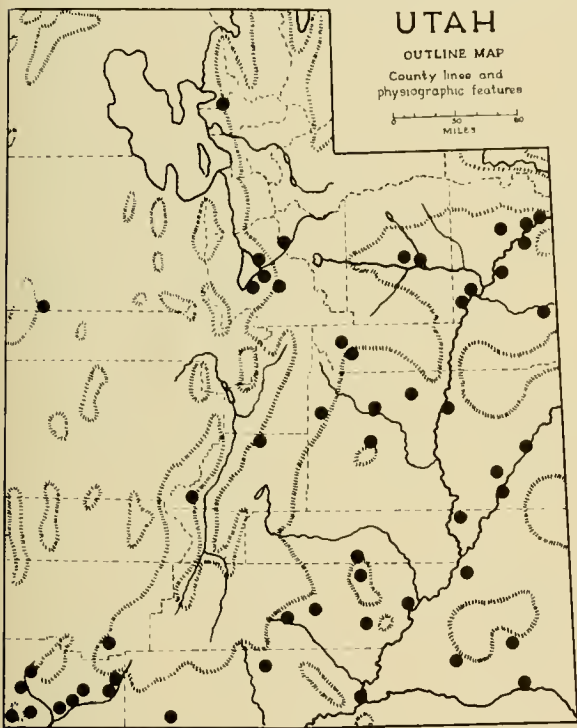


Fig. 32. *Populus fremontii* S. Wats.

Populus fremontii S. Wats. (Fig. 32)

Fremont poplar is almost exclusively a tree of stream-sides and washes throughout the southwest. In Utah it presents an interesting discontinuous pattern of distribution. Although abundant throughout the Colorado River drainage, there are scattered isolated colonies far to the north and west. From Salina Canyon in central Utah to Parry Canyon in the Box Elder County there are groves of Fremont poplar along the water courses in the valleys and foothills. As Bennion, Vickery, and Cottam (1961) indicated, historical records support the present belief that these stands represent native colonies and not pioneer plantings.

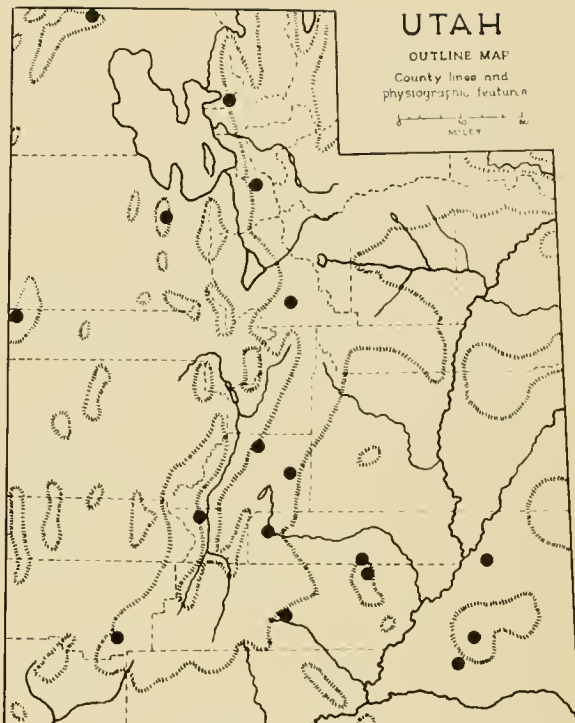


Fig. 33. *Populus angustifolia* x *Populus fremontii*

Occasionally at the mouths of mountain canyons there is a mingling of *P. fremontii* and *P. angustifolia*, a species generally found at higher elevations. Under these conditions one often finds a poplar which is intermediate in characteristics to the two species. Long known as *P. acuminata* (Fig. 33), research by Bennion (1961) has suggested that such plants are actually hybrids between *P. fremontii* and *P. angustifolia*. Specimens of the so-called *P. acuminata* have been found far beyond the northern most stand of *P. fremontii*. It is possible that some of these may represent hybridization between *P. angustifolia* and *P. fremontii* during the altithermal period following the last glaciation when fremont poplar may have had a greater range. Other stands could be hybrids between narrow-leaf cottonwood and other species such as *P. sargentii*. (Bennion, Vickery & Cottam 1961.)

Representative Specimens: *Populus fremontii*: Carbon Co., Castle Dale, *J. Bouns* s.n., May 19, 1963 (NY); Grand Co., Arches Nat'l. Monu., *B.F. Harrison* 11162, April 27, 1947 (BRY); Kane Co., Kanab, *W.P. Cottam* 4319, June 13, 1929 (UT); San Juan Co., Natural Bridges Nat'l. Monu., *P. Rydberg* & *A.O. Garrett* 9484, August 4-6, 1911 (NY); Sevier Co., Pavant Range, *K.S. Erdman* 2705, September 2, 1965 (Weber State College); Uintah Co., Jensen, *E.H. Graham* 7541 & 7540, April 27, 1933 (CM); Utah Co., Utah Lake, *E.M. Christensen* s.n., June 24, 1964 (BRY); Washington Co., St. George, *M.E. Jones* s.n., March 30, 1880 (US).

Representative Specimens: *Populus angustifolia* x *P. fremontii* (previously *P. acuminata*): Box Elder Co., Raft River Mts., *K.S. Erdman* 1491, June 8, 1965 (Weber State College); Garfield Co., Henry Mts., *Stanton* 474, July 15, 1930 (BRY); Iron Co., Cedar Canyon, *W.P. Cottam* 6736, May 9, 1936 (UT); Salt Lake Co., *S. Flowers* 5000, August 8, 1933 (UT); San Juan Co., Natural Bridges Nat'l. Monu., *S.L. Welsh* & *G. Moore* 2864, August 12, 1963 (BRY); Sevier Co.,

Salina Canyon, K.S. Erdman 2928, September 7, 1965 (Weber State College).

Populus tremuloides Michx. (Fig. 34)

Apparently the present climate of Utah is unfavorable for the sexual reproduction of aspen (Moss 1938, Baker 1925). Although some seeds may germinate, the main method of reproduction appears to be root suckering. An aspen stand therefore is usually a clone originating many hundreds of years ago. The vast interconnected root systems lie a few feet under the surface of the ground and at intervals produce sprouts which eventually become independent of the old roots (Gifford 1966, Barnes 1966).

Aspen is very intolerant of shade and therefore yields readily to invading conifers such as white fir, Douglas fir, and ponderosa pine. Although aspen communities may be easily replaced by such conifer stands, continued growth of aspen is favored as long as fire is a common component of its environment. Forest fires kill the conifers but the aspen roots remain alive and suckering will produce a new grove after the fire. Because of the effective fire protection measures used today, many aspen communities throughout the state are now being replaced by conifers.

This species is widespread in Utah as it is throughout temperate North America. Some of the largest specimens of aspen in the United States are located in the Grove of the Aspen Giants in the Manti-La Sal National Forest. There are approximately 20 huge aspen trees with diameters up to three feet. A large

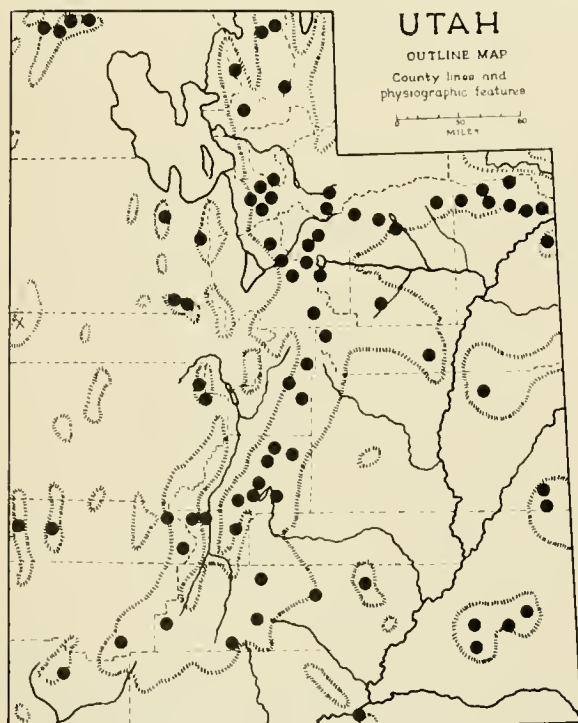


Fig. 34. *Populus tremuloides* Michx.

tree of this species, near Cedar City, is 11 feet in circumference and 75 feet in height (Littlecott 1969, USDA 1969).

Representative Specimens: Beaver Co., Needle Range, S.L. Welsh & G. Moore 3480, August 14, 1964 (BRY); Box Elder Co., Raft River Mts., Preece 903, May 18, 1948 (UT); Cache Co., near Monte Cristo, K.S. Erdman 2599, August 28, 1965 (Weber State College); Garfield Co., Escalante Mts., Beck & Tanner s.n., June 12, 1936 (BRY); Grand Co., Roan Plateau (east) E.H. Graham 9252, June 18, 1935 (CM); Millard Co., Canyon Mts., B.L. Robins 94, August 16, 1913 (USFS); Salt Lake Co., Mill Creek, A.O. Garrett 6098, May 8, 1932 (UT); San Juan Co., Abajo Mts., K.S. Erdman 259, July 29, 1960 (BRY); Sevier Co., Monroe Mt., D.G. Harrington 16, August 10, 1940 (USFS); Uintah Co., Uinta Mts., L.N. Goodding 1215, June 30, 1902 (US); Washington Co., Silver Reef, M.E. Jones 5169, May 5, 1894 (US).

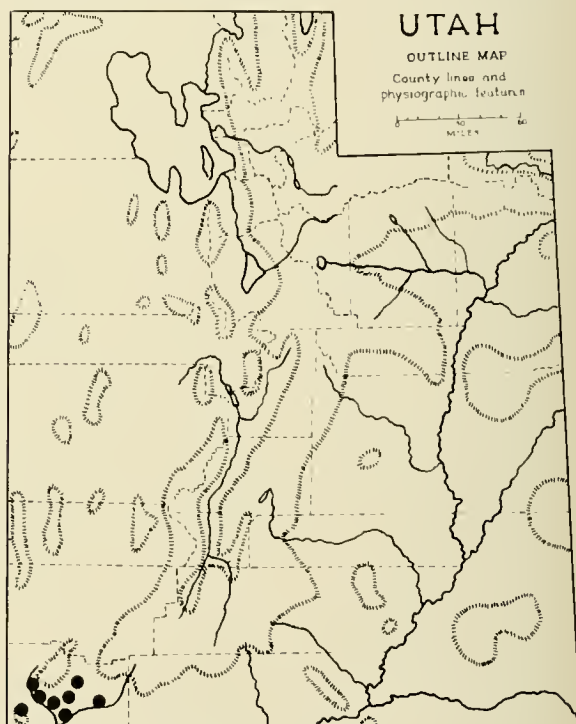


Fig. 35. *Prosopis glandulosa* Torr.

Prosopis glandulosa Torr. (Fig. 35)

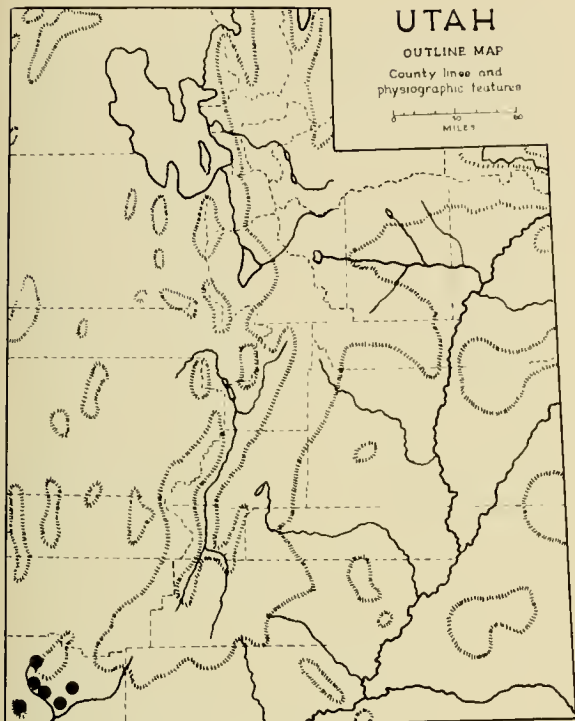
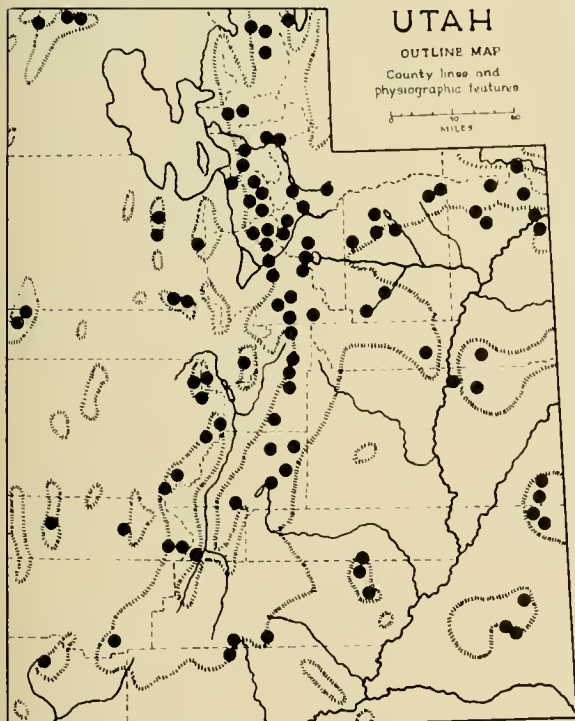
Mesquite is a very common plant in the southwest, and is an aggressive invader of disturbed land. In Texas it has spread over millions of acres of grazing land. In Utah it is restricted to the valley of the Virgin River.

Representative Specimens: Washington Co., St. George, W.W. Eggleston 14799, September 7-12, 1918 (US); Washington Co., Rockville, K.S. Erdman 63, May 11, 1960 (BRY).

Prosopis pubescens Benth. (Fig. 36)

The Fremont screwbean, so named because of the tightly coiled nature of its fruit, is a small shrubby tree of the Virgin River basin in Washington County. It is less common than *P. glandulosa*.

Representative Specimens: Washington Co., Beaver Dam Mts., L.C. Higgins 818, August 19, 1966 (BRY); Washington Co., Santa Clara, W.P. Cottam 3396, June 21, 1928 (BRY).

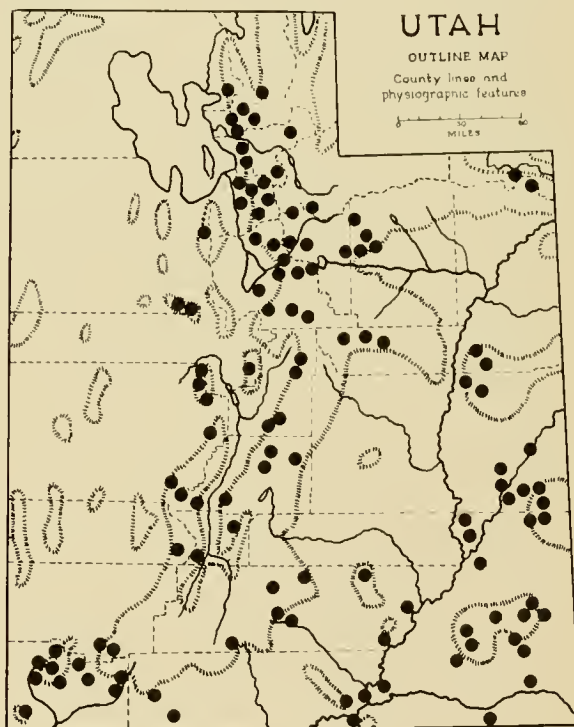

 Fig. 36. *Prosopis pubescens* Benth.

 Fig. 37. *Prunus virginiana* L. var. *melanocarpa* (A. Nels.) Moldenke

Prunus virginiana L. var. *melanocarpa* (A. Nels.) Moldenke (Fig. 37)

Chokecherry is found throughout Utah's mountains in a variety of habitats. Under favorable condi-

tions it may form large streamside groves where the trunks are many inches in diameter. However, it is also an early invader of talus slopes where plants, a foot or two in height, may be many years old.

Representative Specimens: Beaver Co., Wah Wah Mts., S. Welsh & E.M. Christensen 2692, September 13, 1963 (BRY); Box Elder Co., Raft River Mts., K.S. Erdman 1527, June 8, 1965 (Weber State College); Duchesne Co., Rock Creek, J. Brotherson 904, June 19, 1965 (BRY); Garfield Co., Bryce Canyon, H. Buchanan 165, July 3, 1957 (UT); Garfield Co., Henry Mts., R. McVaugh 14491, June 7, 1953 (NY); Grand Co., Roan Plateau (east), E.H. Graham 9862, July 28, 1935 (CM); Juab Co., Deep Creek Mts., W.P. Cottam 8189, June 16, 1940 (UT); Piute Co., Tushar Mts., K.S. Erdman 26, May 9, 1960 (BRY); Rich Co., Bear Lake, L.K. Henry s.n., June 21, 1956 (CM); San Juan Co., Abajo Mts., P. Rydberg & A.O. Garrett 9668, August 1911 (NY); San Pete Co., Ephraim, I. Tidestrom 2442, July 14, 1909 (US); Tooele Co., Sheeprock Mts., N. Frischknecht 64, June 1, 1961 (USFS); Wasatch Co., Deer Creek, R.H. Foster 224, October 10, 1964 (BRY); Weber Co., Ogden Canyon, A.E. Hitchcock 1479, August 19, 1913 (US).


 Fig. 38. *Quercus gambelii* Nutt.

Quercus gambelii Nutt. (Fig. 38)

Gambel oak forms great belts which extend for hundreds of miles along the foot hills of mountain ranges in Utah. It is a common member of the mountain brush zone where it is usually associated with maples, chokecherry, mountain mahogany, and other species. It is generally a small tree, and often little more than a shrub, but under favorable conditions the stems are often over a foot in diameter.

The most common method of reproduction in Gambel oak is through root suckering, but there is some reproduction by acorn. Thus large oak clones are common on the mountainsides and may be several

hundred years in age. The expansion of the clone is slow, perhaps as little as a foot is added to the margin per year. There is some evidence that Gambel oak is far more widespread now than it was a hundred years ago. (Christensen 1950.)

The northern-most stands of Gambel oak are in Parry Canyon and near Mantua in southern Box Elder County, and Little Bear Canyon, Cache County. However, it appears that these may represent considerable extension of the range in the past hundred years. Ferris, a very careful reporter, indicated that oak was not present in Ogden Hole (Huntsville Valley), Weber County in 1830 but today it is abundant on the foothills. (Christensen 1950.)

Q. gambelii is generally not a species of the basin and range province in Utah, but it is present in the Mineral, Canyon, Sheeprock, and Oquirrh Mountains. Some of these colonies may be of great age, but Christensen (1950) suggests that others may have resulted from recent introduction of acorns by squirrels or other animals.

Gambel oak has long presented problems to the taxonomist. It is high variable species, which has been alternately considered as one species or treated as several species or subspecific taxa. (Rydberg 1922, Tucker 1961a). Today it is generally regarded as a highly polymorphic species which has hybridized readily with other oaks throughout the southeast.

The discovery in 1954 (Cottam & Drobnick 1955) of an unusual oak clone in the Oquirrh Mountains of

northern Utah led to the study of its relationship to the Gambel oak with which it was associated to *Q. turbinella* of southern Utah which it resembled. It was determined that the unusual clone was a hybrid between these two oaks, a conclusion full of interesting implications inasmuch as one parental species, *Q. turbinella* is 300 miles to the south (Cottam & Tucker 1956). The name proposed for this hybrid was *Quercus x pauciloba* (Tucker 1961a).

Further studies revealed similar hybrid clones scattered from Ogden south to St. George and Arizona. It was postulated that during the altithermal period following the most recent glaciation, temperatures may have been such that *Q. turbinella* grew far north of its present range and hybridized with Gambel oak. If so, some hybrid clones may be several thousand years in age. The distribution map (Fig. 39), for *Q. x pauciloba* is based on specimens cited by Tucker (1961b).

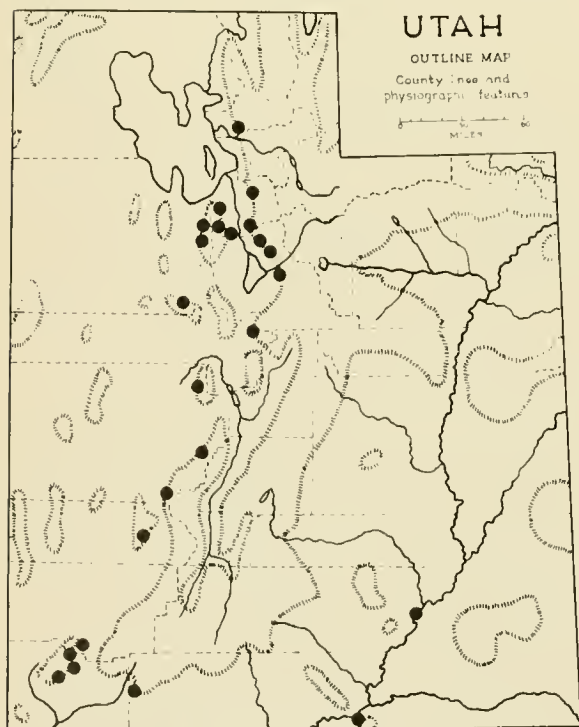


Fig. 39. *Quercus x pauciloba* Rydb.

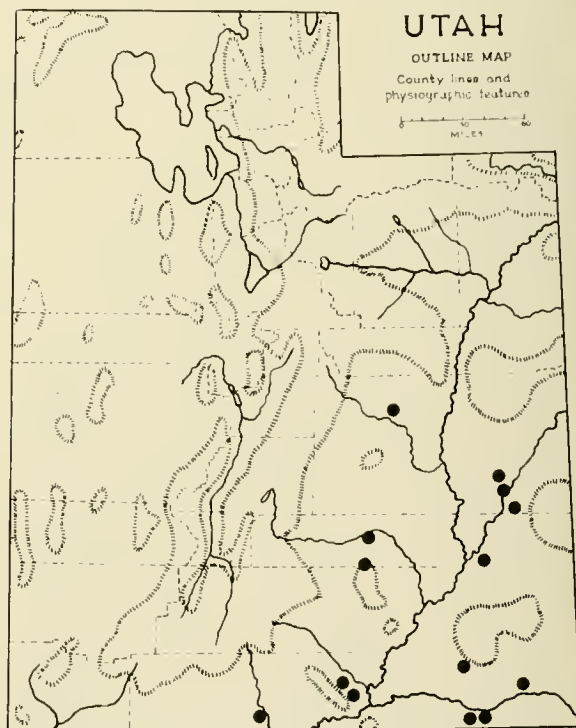


Fig. 40. *Quercus undulata* Torr.

This particular study helped focus renewed attention on the taxonomic problems of a common shrubby oak of southeastern Utah, long identified as *Q. undulata* (Fig. 40). As Tucker pointed out (1961a), the taxonomic history of this species is very confused and troublesome. He proposed that this highly polymorphic group represents hybrids between *Q. gambelii* and a number of other oaks throughout the southwest. *Q. x pauciloba* represented hybrids between *Q. gambelii* and *Q. turbinella* and these were most common along the western limits of Gambel oak's range. On the other hand, there was little evi-

dence that *Q. turbinella* was a parent of the sprawling oak of southeastern Utah. Tucker suggested that *Q. havardii*, a low, rhizomatous shrub of sandy areas in Texas and New Mexico, had crossed with Gambel oak to produce what has long been called *Q. undulata* in Utah. (Tucker 1961a, 1961b.)

Representative Specimens: *Quercus gambelii*: Box Elder Co., Parry Canyon, E.M. Christensen s.n., July 20, 1948 (UT); Cache Co., Little Bear Canyon, Bancroft 1031, June, 1928 (UT); Carbon Co., Book Cliffs, E.H. Graham 8339a, June 28, 1933 (CM); Duchesne Co., Red Creek, J. Brotherson 507, June 21, 1965 (BRY); Garfield Co., Aquarius Plateau, Beck & Tanner s.n., June 23, 1936 (BRY); Grand Co., La Sal Mts., K.S. Erdman 197, July 27, 1960 (BRY); Kane Co., Kanab, B.F. Harrison 11087, August 27, 1946 (BRY); Salt Lake Co., Emigration Canyon, Vickery 2516, August 30, 1959 (Utah); San Juan Co., Abajo Mts., W.P. Cottam 14392, July 11, 1956 (UT); San Juan Co., Aztec Creek, Lindsay 154, July 25, 1958 (UT); San Pete Co., Mt. Pleasant, I. Tidestrom 1867, September 2, 1908 (US); Sevier Co., Salina Canyon, M.E. Jones 5447, June 16, 1894 (US); Tooele Co., Sheeprock Mts., W.P. Cottam 14340, July 1, 1956 (UT); Uintah Co., Roan Plateau (east), E.H. Graham 9825, July 26, 1935 (CM); Washington Co., Beaver Dam Mts., L.C. Higgins 663, May 27, 1966 (BRY).

Representative Specimens: *Quercus x pauciloba* (taken from Tucker 1961b): Beaver Co., Mineral Mts., Drobnick 86 (UT); Iron Co., four mi. NW of Kanarrville, 6,000 ft., Cottam & Drobnick 14760 (UT); Juab Co., Wasatch Mts., Drobnick 63 (UT); Salt Lake Co., Oquirrh Mts., Drobnick 1 (UT).

Representative Specimens: *Q. undulata*: Emery Co., San Rafael Swell, M.E. Jones s.n., May 28, 1914 (US); Grand Co., Pritchett Canyon, P.A. Rydberg & J.O. Garrett 8506, July 3, 1911 (US); Kane Co., Cockscomb Ridge, S.L. Welsh 5334, May 6, 1966 (BRY); San Juan Co., Monument Valley, H.C. Cutler 2990, August 28, 1939 (US).

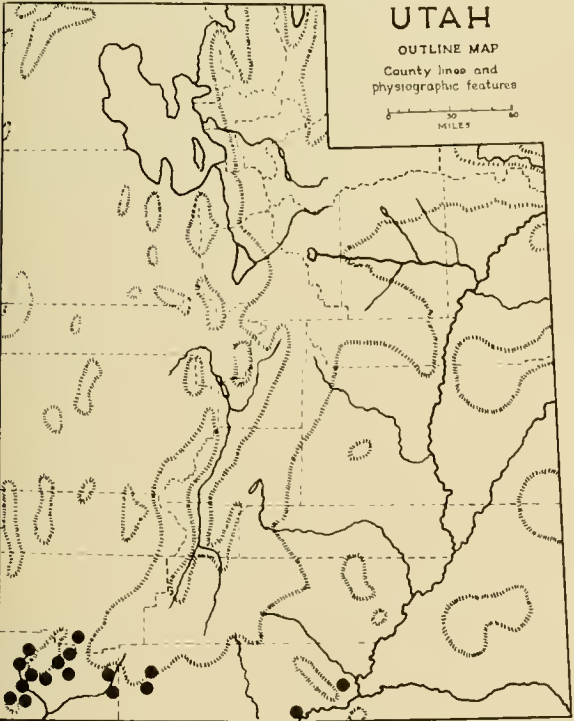


Fig. 41. *Quercus turbinella* Greene

Quercus turbinella Greene (Fig. 41)

On first glance at the small evergreen holly-like leaves, most Utahans would be surprised that this

species is an oak. Characteristic of dry hillsides and canyons of extreme southwestern Utah, its rounded, blue-green form gives a distinctive cast to the areas where it is common.

The northern limits of this species today is just over the Great Basin divide in the vicinity of Kanarrville, but there is some indication that this live oak once thrived as far north as Salt Lake City and Ogden. *Q. turbinella* hybridizes freely with *Q. gambelii* in Washington County and intermediate forms are common. The discovery of similar hybrid clones identical to these far to the north in the Oquirrh Mountains and elsewhere led botanists to suggest that during the period of higher temperatures following the most recent glaciation *Q. turbinella* grew in northern Utah and hybridized with *Q. gambelii*. As temperatures dropped, the live oak died out and only the hybrid clones remained. (Cottam, Tucker, and Drobnick 1959.)

Representative Specimens: Iron Co., Kanarrville, Drobnick 14758, September 5, 1957 (UT); Kane Co., Dance Hall Rock, J.R. Murdock 381, May 2, 1961 (BRY); Kane Co., Glendale, W.P. Cottam 14626, September 6, 1958 (UT); Washington Co., Beaver Dam Mts., I. Tidestrom 9329, May 9, 1919 (US).

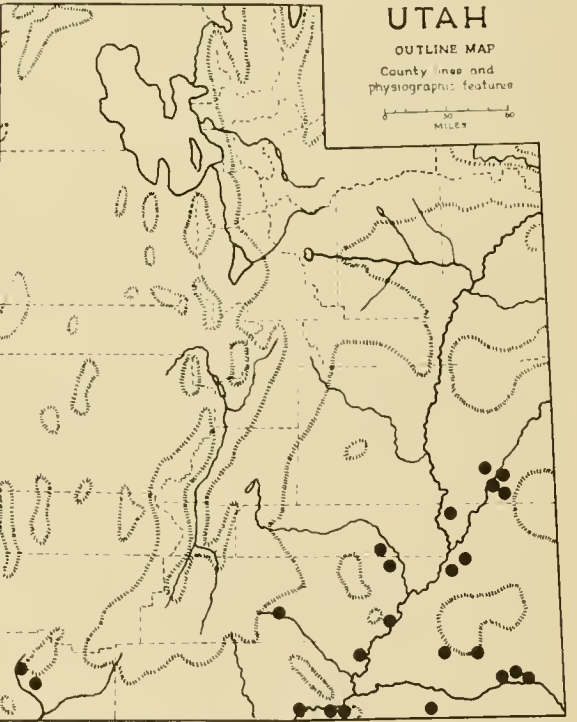


Fig. 42. *Rhamnus betulaeifolia* Greene

Rhamnus betulaeifolia Greene (Fig. 42)

Birch-leaf buckthorn is one of two species of *Rhamnus* present in Utah. The other, *R. alnifolia*, has recently been discovered in Big Cottonwood Canyon near Salt Lake City. However, it is a shrub and out of the scope of this work. *R. betulaeifolia*, on the other hand, is a small tree widely distributed in the

rugged canyon country of the Colorado drainage from Moab to the south. It is also present in Washington County.

Representative Specimens: Grand Co., Arches Nat'l. Monu., *S.L. Welsh* & *G. Moore* 2760, September 28, 1963 (BRY); San Juan Co., Bluff, *A.H. Holmgren* & *W.S. Boyle* & *D. Will* 7803, July 18, 1948 (US); San Juan Co., Rainbow Bridge, *H.C. Culter* 2868, August 3, 1939 (NY); Washington Co., Washington Flat, *W.P. Cottam* 8815, June 18, 1941 (UT).

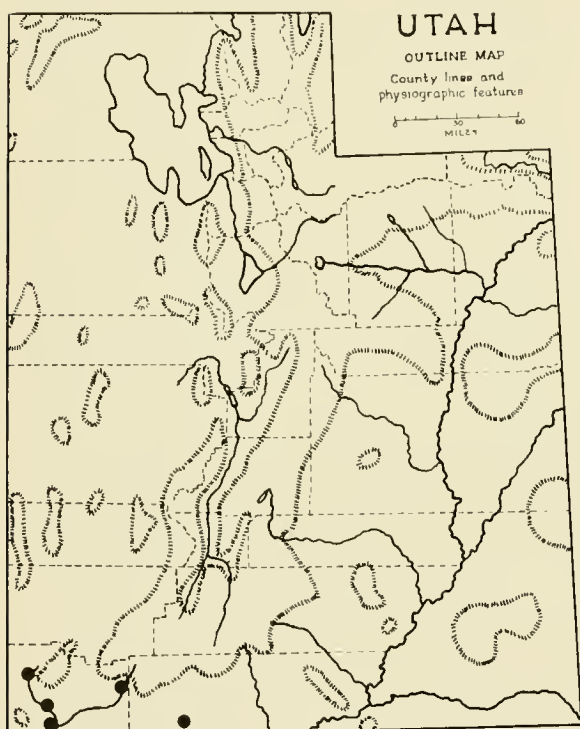


Fig. 43. *Robinia neomexicana* A. Gray

Robinia neomexicana A. Gray (Fig. 43)

The New Mexico locust is a small tree of the southwest which is restricted to southern Utah (Washington and Kane Counties) where it grows in washes and on moist slopes.

Representative Specimens: Kane Co., Kanab, *Greenhalgh* s.n., May 21, 1947 (UT); Washington Co., Gunlock, *Plummer* 7323, May 14, 1939 (UT); Washington Co., Zion Nat'l. Park, *A.H. Barnum* 1247, May 31, 1964 (BRY).

Salix amygdaloides Andersson (Fig. 44)

Peach-leaf willow is a common streamside tree of northern Utah, especially along the Wasatch Front and in the Uinta Basin. Elsewhere in the state the distribution is spotty.

Representative Specimens: Beaver Co., Milford, *L.N. Goodding* 1019, June 4, 1902 (NY); Box Elder Co., Bear River, *A. Wetmore* 336, May 23, 1915 (US); Duchesne Co., Duchesne, *A.D. Youngberg* 712, May 27, 1966 (BRY); Salt Lake Co., Salt Lake City, *A.O. Garrett* 7657, May 29, 1938 (UT); San Juan Co., Green River, *A. Cronquist* 8992, May 10, 1961 (NY); Uintah Co., Roan Plateau (east), *N.H. Holmgren* 1900, June 11, 1965 (NY); Utah Co., Utah Lake, *E.M. Christensen* s.n., June 24, 1964 (BRY).

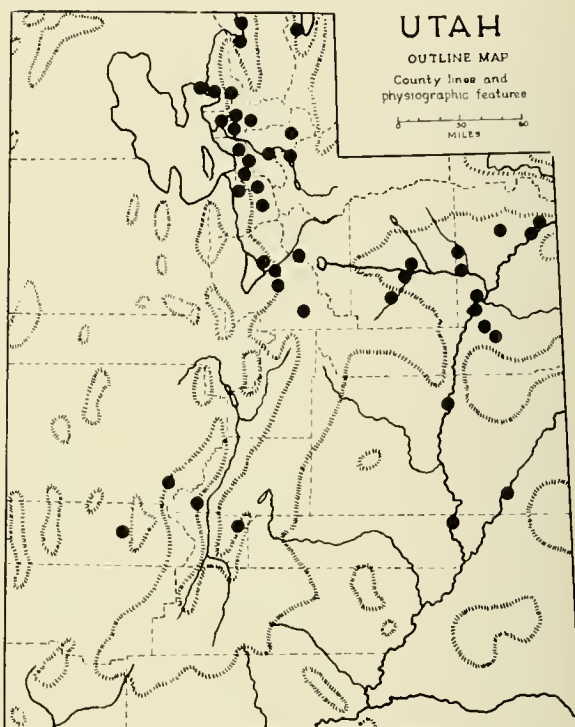


Fig. 44. *Salix amygdaloides* Andersson

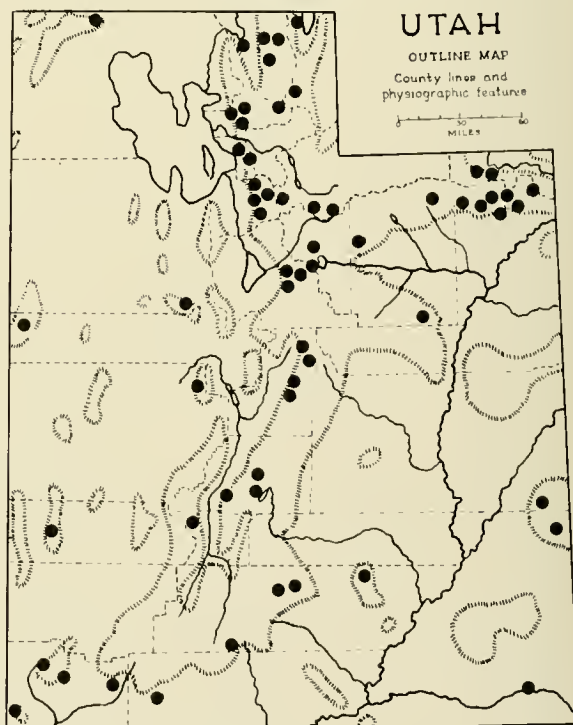


Fig. 45. *Salix bebbiana* Sarg.

Salix bebbiana Sarg. (Fig. 45)

Bebb willow is widespread throughout the United States. In Utah it is present on most mountain ranges. This species is not as restricted to streamside as

many other willows, but is found on drier mountain slopes and as an understory tree in coniferous forests at elevations from 6,000 to 10,000 feet. (Youngberg 1966.)

Representative Specimens: Beaver Co., Wah Wah Mts., *S. Welsh & E.M. Christensen* 2691, September 13, 1963 (BRY); Box Elder Co., Raft River Mts., *W.P. Cottam* 2970, June 5, 1928 (UT); Duchesne Co., Red Creek, *E.H. Graham* 9435, June 26, 1935 (CM); Garfield Co., Henry Mts., *Stanton* 341, July 12, 1930 (UT); Grand Co., La Sal Mts., *B. Maguire* 1718, June 26, 1932 (UT); Juab Co., Deep Creek Mts., *Beecraft* 374, June 28, 1932 (UT); Rich Co., Bear Lake, *A.D. Youngberg* 734, June 12, 1966 (BRY); Salt Lake Co., City Creek, *M.E. Jones* s.n., June 3, 1880 (US); San Pete Co., New Canyon, *J.A. Willey* 371, June 2, 1913 (USFS); Sevier Co., Glenwood, *L.F. Ward* 194, June 12, 1875 (US); Tooele Co., Sheeprock Mts., *J. Leetham* 80, August 19, 1966 (BRY); Uintah Co., Brush Creek, *L.N. Goodding* 1283, July 7, 1902 (NY); Washington Co., Pine Valley Mts., *Gould* 1780, May 26, 1942 (UT); Weber Co., Snow Basin, *A.D. Youngberg* 364, September 9, 1965 (BRY).

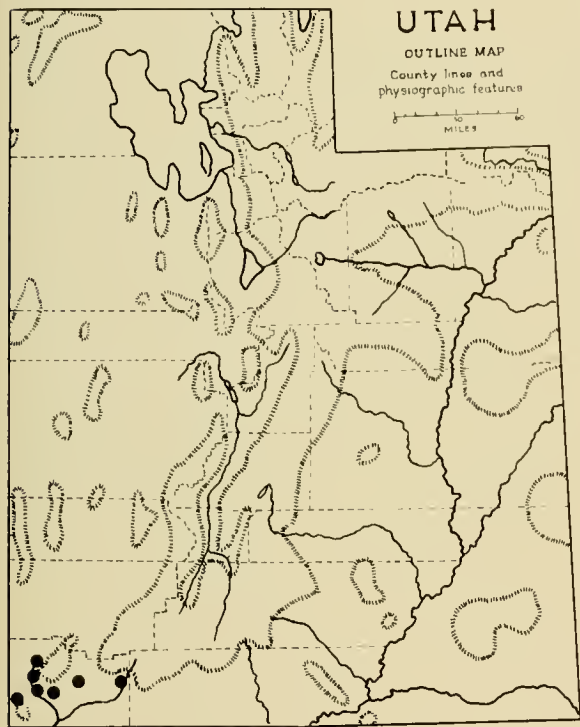


Fig. 46. *Salix laevigata* Bebb.

Salix laevigata Bebb. (Fig. 46)

For many years this species was reported to be present in the Colorado River canyons of eastern Utah. However, Youngberg (1966) indicated that all specimens from that area which he had observed were misidentified and that the smooth willow is limited to Washington Co.

Representative Specimens: Washington Co., Beaver Dam Mts., *L.C. Higgins* 426, April 9, 1966 (BRY); Washington Co., Santa Clara Creek, *W.P. Cottam* 3370, June 21, 1928 (UT).

Salix lasiandra Benth var. *caudata* (Nutt.) Sudworth (Fig. 47)

Pacific willow is widespread from Alaska to New

Mexico and is common throughout Utah up to elevations of 8,000 feet, where it occurs along the margins of streams and reservoirs.

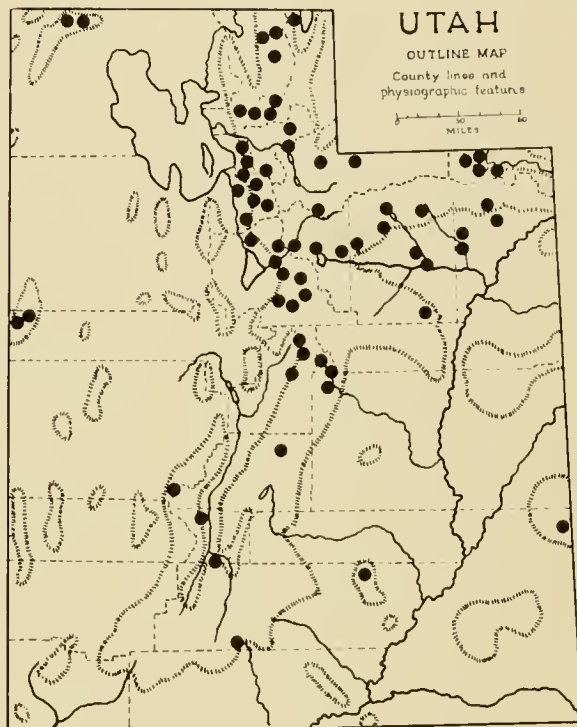


Fig. 47. *Salix lasiandra* Benth. var. *caudata* (Nutt.) Sudworth

Representative Specimens: Box Elder Co., Raft River Mts., *W.P. Cottam* 2972, June 5, 1928 (UT); Daggett Co., Sheep Creek, *S. Flowers* 173, July 25, 1959 (UT); Duchesne Co., Moon Lake, *E.H. Graham* 9371, June 25, 1935 (CM); Emery Co., Huntington Canyon, *A.D. Youngberg* 424, September 11, 1935 (BRY); Garfield Co., Bryce Canyon, *Buchanan* 465, June 28, 1959 (UT); Juab Co., Deep Creek Mts., *B. Maguire* 21929, July 14, 1943 (UTC); Piute Co., Kingston, *M.E. Jones* 5322k, May 20, 1894 (US); Rich Co., Bear Lake, *A.D. Youngberg* 736, June 12, 1966 (BRY); San Juan Co., La Sal Mts., *R. E. Mellenstins* 31, September 2, 1916 (USFS); Utah Co., Provo Canyon, *A.D. Youngberg* 613, October 2, 1965 (BRY).

Salix lasiolepis Benth. (Fig. 48)

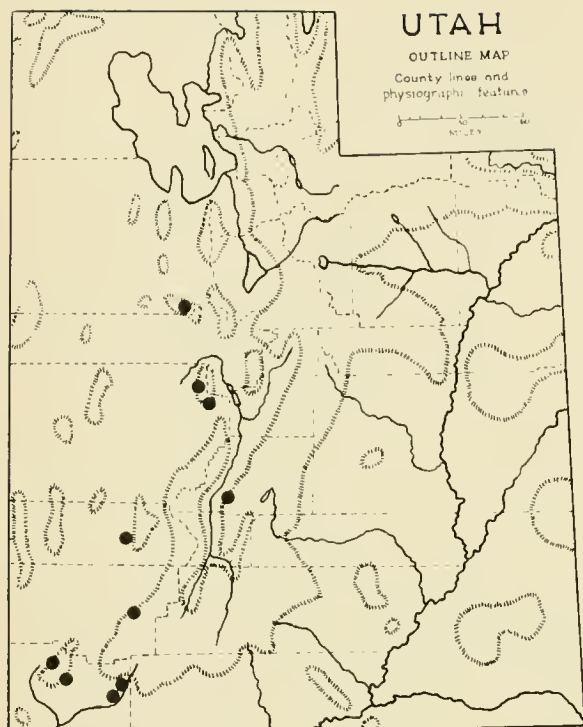
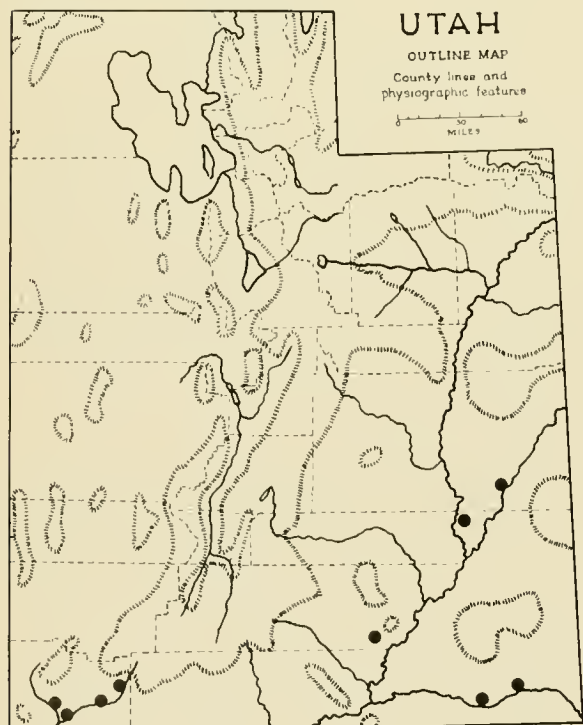
This willow grows along streams and in wet areas in Utah, where it is of infrequent occurrence.

Representative Specimens: Iron Co., Parowan, *W.W. Eggleston* 14903, September 17, 1918 (US); Millard Co., Canyon Mts., *K.S. Erdman* 134, May 13, 1960 (BRY); Sevier Co., Monroe Mt., *K.S. Erdman* 5, May 9, 1960 (BRY); Washington Co., Pine Valley, *F.W. Gould* 1781, May 26, 1942 (NY).

Salix nigra Marsh (Fig. 49)

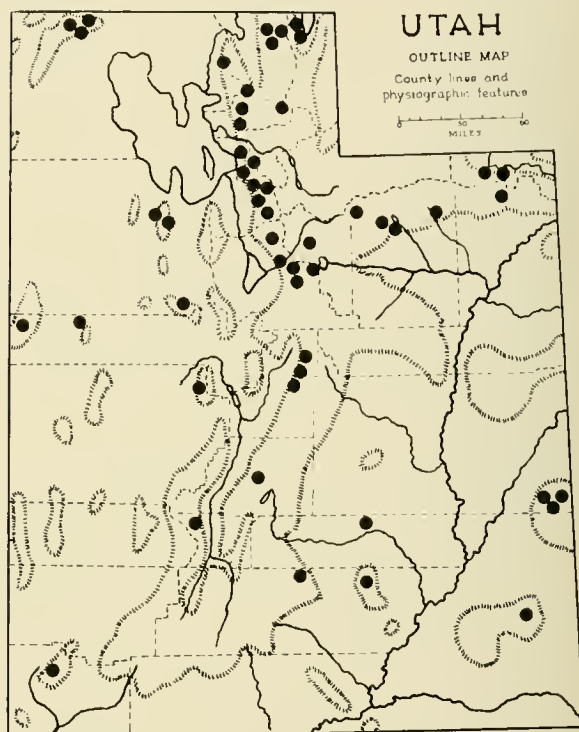
Western black willow is restricted to streambanks in Washington County and the Colorado River drainage in eastern Utah. It extends as far north as Moab in Grand County.

Representative Specimens: Garfield Co., Bullfrog Creek, *S. Welsh* 3969, May 6, 1965 (BRY); Grand Co., Arches Nat'l. Monu., *S. Welsh* 2820, May 30, 1965 (BRY); Washington Co., St. George, *W.W. Eggleston* 14773, September 7-12, 1918 (US).

Fig. 48. *Salix lasiolepis* Benth.Fig. 49. *Salix nigra* Marsh*Salix scouleriana* Barratt (Fig. 50)

Scouler or fire willow, like Bebb willow, is widespread throughout Utah and not limited to stream-sides. It is a common understory tree or shrub in con-

iferous or aspen forests. Its altitudinal range is from 5,000 to 11,000 feet elevation.

Fig. 50. *Salix scouleriana* Barratt

Representative Specimens: Box Elder Co., Raft River Mts., *W.P. Cottam* 2949, June 5, 1928 (BRY); Cache Co., Logan Canyon, *C.R. Ball* 1866, August 18, 1914 (US); Daggett Co., Red Canyon, *L. Williams* 593, June 10, 1932 (NY); Davis Co., Farmington Canyon, *A.D. Youngberg* 527, September 3, 1965 (BRY); Garfield Co., Henry Mts., *Stanton* 188, June 29, 1930 (UT); Grand Co., La Sal Mts., *K.S. Erdman* 211, July 27, 1960 (BRY); Juab Co., Deep Creek Mts., *B. Maguire* 2533a, June 20, 1933 (UTC); San Juan Co., Abajo Mts., *B. Maguire* 1722a, July 1, 1932 (UTC); San Pete Co., Mt. Pleasant, *I. Tidestrom* 1912, September 4, 1908 (US); Tooele Co., Stansbury Mts., *E.M. Christensen* s.n., July 29, 1963 (BRY); Utah Co., Provo Canyon, *S. Welsh* 3385, August 5, 1964 (BRY); Washington Co., Pine Valley Mts., *B. Maguire* 20184, August 1, 1934 (UTC).

Sambucus caerulea Raf. (Fig. 51)

This elderberry is common throughout most of Utah's mountains. This shrubby plant is common among stands of ponderosa pine, Douglas fir, and aspen, especially in more open areas near streams.

Representative Specimens: Beaver Co., Needle Range, *S.L. Welsh & G. Moore* 3202a, July 18, 1964 (BRY); Carbon Co., Roan Plateau (west), *S.L. Welsh & E.M. Christensen* 6564, August 11, 1967 (BRY); Duchesne Co., Moon Lake, *E.H. Graham* 6410, June 30, 1931 (CM); Garfield Co., Bryce Canyon, *H. Buchanan* 183, July 9, 1957 (UT); Grand Co., *B. Maguire* 21716, July 15, 1933 (NY); Salt Lake Co., Emigration Canyon, *Vickery* 2514, August 30, 1959 (UT); San Pete Co., Ephraim Canyon, *I. Tidestrom* 138, August 12, 1907 (US); Sevier Co., Tushar Mts., *R.G. Warnock* s.n., July 7, 1961 (BRY); Tooele Co., Stansbury Island, *W.P. Cottam* 9174, July 7, 1942 (UT); Uintah Co., Dinosaur Nat'l. Monu., *A.H. Holmgren* 14248, June 29, 1962 (NY); Utah Co., Provo Canyon, *S.L. Welsh* 3243, June 1964 (BRY); Washington Co., Bellvue, *I. Tidestrom* 9412, May 10, 1919 (USFS); Weber Co., North Fork, *Czll* 89, July 26, 1940 (UT).

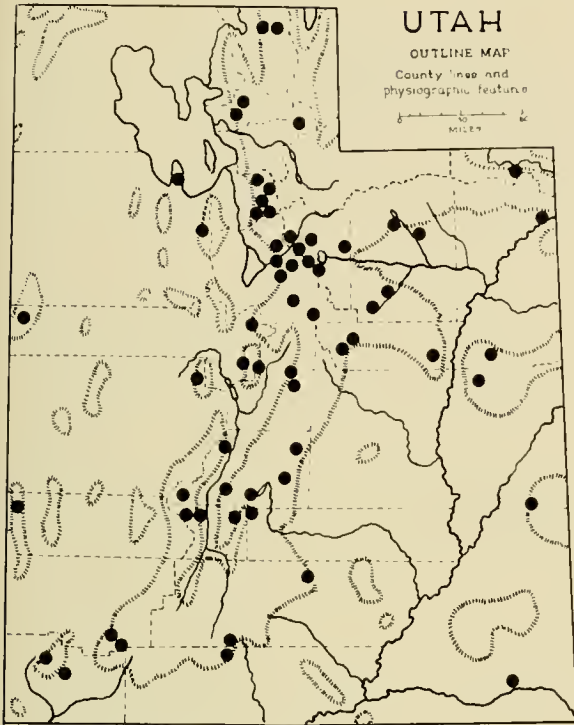


Fig. 51. *Sambucus caerulea* Raf.

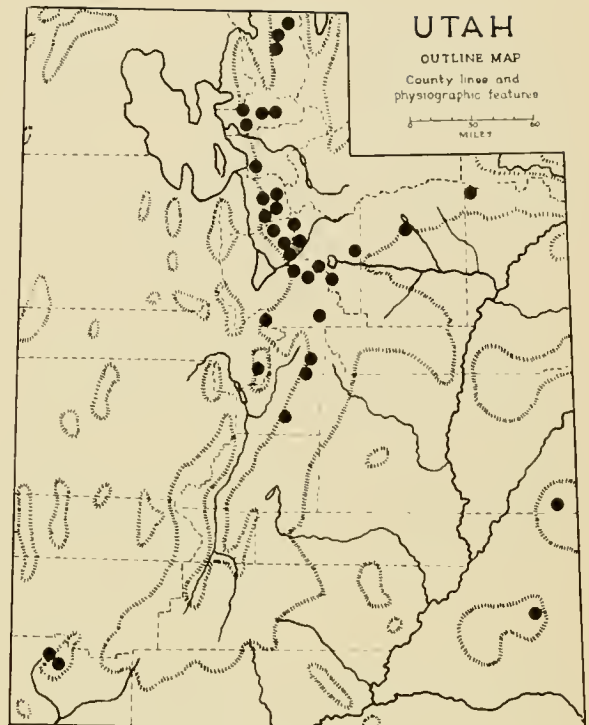


Fig. 53. *Sorbus scopulina* Greene

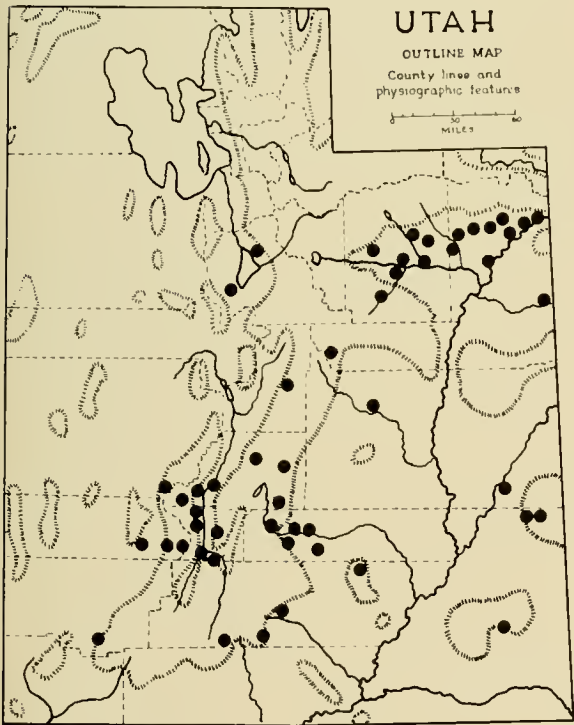


Fig. 52. *Shepherdia argentea* (Pursh) Nutt.

Shepherdia argentea (Pursh) Nutt. (Fig. 52)
The silver buffaloberry has a spotty distribution in Utah. It is common in the Uinta Basin and in the central plateaus, especially along the Sevier River.

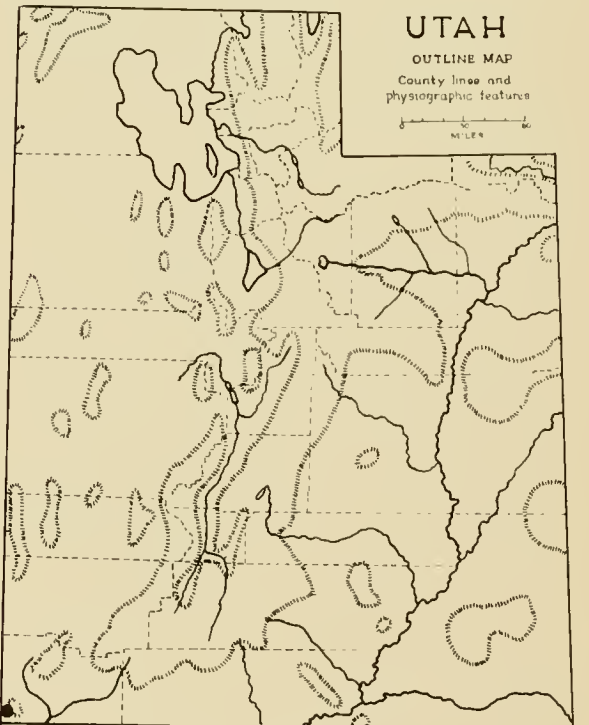


Fig. 54. *Yucca brevifolia* Engelm.

There are a few scattered records from the isolated ranges of the eastern part of the state and Utah Valley. Except for the Mineral Mountains, it is absent in the basin and range province.

Representative Specimens: Carbon Co., Gordon Creek, *S. Flowers*, s.n., September 14, 1933 (UT); Duchesne Co., Roan Plateau (west), *J.A. Willey* 63, May 23, 1918 (USFS); Garfield Co., Escalante Mts., *B. Maguire* s.n., August 8, 1934 (NY); Iron Co., Cedar City, *M.E. Jones* 5204, May 10, 1894 (US); Piute Co., Marysvale, *P.A. Rydberg & E.C. Carlton* 6958, July 19, 1905 (US); San Juan Co., La Sal Mts., *B. Maguire* s.n., August 17, 1934 (NY); Uintah Co., Ashley Creek, *E.H. Graham* 9812, July 23, 1935 (CM); Utah Co., Geneva, *W.P. Cottam* 230, July 19, 1925 (BRY); Wayne Co., Bicknell, *Vickery* 591, May 19, 1956 (UT).

Sorbus scopulina Greene (Fig. 53)

This small, shrubby tree, known as mountain ash, has a disjunct distribution throughout the state. It is common only in certain areas such as the Wasatch Mountains, but extends southward into the Wasatch Plateau and San Pitch Mountains. It has also been found in the Uinta Basin, and the La Sal, Abajo, and Pine Valley Mountains. Evidently mountain ash is absent in the basin and range provinces.

DISCUSSION

There are several basic problems associated with any study of the distribution of the native trees of Utah. One problem involves the lack of herbarium specimens. This is especially true for the Pinaceae. For example, when I began this research in 1959 I found only nine specimens of *Picea engelmannii* from Utah in the herbaria of the three universities of the state. This perhaps reflects a tendency of collectors to avoid tree species, especially conifers. Such specimens are bulky, dry slowly, and in the case of spruces, lose their leaves. The number of specimens in the Utah herbaria has increased measurably in the past decade due to the field collecting a number of botanists.

Another problem related to distributional studies is the varied topography of the state. Many of Utah's mountains are remote, rugged, and difficult to botanize. There is limited collecting data for species growing near timberline (e.g. *Pinus aristata*, *P. flexilis*, *Picea engelmannii*, and *Abies lasiocarpa*). There is a need for much more field work on the mountain summits and upper slopes throughout the state. Much of the broken canyon country of the Colorado Plateau has been all but inaccessible until the past decade when mapping and prospecting began in real earnest. Thus our records of *Ostrya knowltonii* and other species are of recent origin.

The most rigorously collected regions of the state are near population centers in Cache, Salt Lake, and Utah Counties. Surprisingly the plants of Davis and Weber Counties have been poorly sampled but the rapid growth of Weber State College has resulted in an active collecting program which may correct this deficiency. Because Washington County includes some of Utah's most spectacular scenery and has the lowest elevations in the state, this area has been of great interest for years. The low land regions have

Representative Specimens: Cache Co., Tony Grove Lake, *A.R. Standing* 51, September 16, 1923 (USFS); Grand Co., La Sal Mts., *C.A. Purpus* 7039, August, 1899 (U.S.); Juab Co., Mt. Nebo, *P. Rydberg & E.C. Carlton* 7576, August 15, 1905 (NY); Salt Lake Co., Emigration Canyon, *W.P. Cottam* 9157, September 10, 1942 (UT); San Juan Co., Abajo Mts., *K.S. Erdman* 237, July 28, 1960 (BRY); Uintah Co., Dry Fork Creek, *E.H. Graham* 8397, July 5, 1933 (CM); Washington Co., Pine Valley Mts., *O.A. Olsen* 349, August 13, 1929 (USFS); Weber Co., Ogden Canyon, *A.E. Hitchcock* 1449, August 19, 1913 (US).

Yucca brevifolia Engelm. (Fig. 54)

Joshua trees grow only on the southwestern slope of the Beaver Dam Mountain and in Beaver Dam Wash in Washington County. It is perhaps the most distinctive tree in the state with its awkward branching and long, stiff, dagger-like leaves. Some authors (Little 1950; Kearny & Peebles 1951) have considered the smaller form found in Utah and adjoining Nevada as a distinct variety.

Representative Specimen: Washington Co., Beaver Dam Wash, *S.L. Welsh* 1474, April 8, 1961 (BRY).

been well collected, but the uplands such as the Pine Valley Mountains have been somewhat neglected.

While the Abajo, La Sal, and Henry Mountains in eastern Utah have received considerable attention, the high broken southern border of the Uinta Basin known as the Roan or Tavaputs Plateau needs much more work. Most neglected of all, however, are ranges of the Great Basin such as the House and Confusion Ranges where little collecting has been done.

Tables 1 through 41 list the tree species for each of the major topographic units of Utah. Species starred (*) are reported to occur in that area. There are herbarium records for all other species.

After studying the distribution maps, several basic patterns emerge. Certain trees, *Yucca brevifolia* and *Acacia greggii*, are typical of the Lower Sonoran Desert and occur only in Beaver Dam Wash, the lowest and most southwestern part of the state. Other southwestern desert species are a little more widespread but are still restricted to Washington and perhaps Kane Counties. These are *Salix laevigata*, *Quercus turbinella*, *Robinia neomexicana*, *Prosopis glandulosa*, *P. pubescens*, *Fraxinus velutina*, and *Chilopsis linearis*. Other desert species more common in the Colorado River canyon-lands are *Cercis canadensis*, *Ostrya knowltonii*, *Rhamnus betulaeifolia*, *Salix nigra*, *Celtis reticulata*, and *Fraxinus anomala*.

Another conspicuous distributional pattern is portrayed by *Pinus ponderosa*, *P. edulis*, *Populus fremontii*, and *Quercus gambelii*. All of these species are uncommon or absent from the Great Basin and reach their northern limits in Utah in the Wasatch and Uinta Mountains.

Only one species, *Pinus monophylla*, is restricted primarily to the Great Basin and only *Pinus contorta* is limited to extreme northern Utah. A few other spe-

cies are uncommon or at least very spotty in occurrence. Among these are *Pinus aristata*, *Sorbus scopulina*, *Piceapungens*, *Alnus tenuifolia*, and *Shep-*

herdia argentea. The remainder of Utah's trees are generally widespread throughout the state, at least in mountainous regions.

TABLES

Table 1. Abajo Mountains and Elk Ridge, 11,360 ft.

- Gymnosperms
- Abies concolor*
 - Abies lasiocarpa**
 - Juniperus osteosperma*
 - Juniperus scopulorum*
 - Picea engelmannii*
 - Pinus edulis*
 - Pinus ponderosa*
 - Pseudotsuga mensiesii*

- Angiosperms
- Acer glabrum*
 - Acer grandidentatum*
 - Acer negundo*
 - Alnus tenuifolia*
 - Betula occidentalis*
 - Celtis reticulata*
 - Cercocarpus ledifolius*
 - Cercocarpus montanus*
 - Fraxinus anomala*
 - Populus angustifolia*
 - Populus fremontii*
 - Populus tremuloides*
 - Prunus virginiana*
 - Quercus gambelii*
 - Rhamnus betulaeifolia*
 - Salix scouleriana*
 - Shepherdia argentea*
 - Sorbus scopulina*

Table 2. Aquarius Plateau (Escalante & Boulder Mountains), 11,328 ft.

- Gymnosperms
- Abies concolor*
 - Abies lasiocarpa*
 - Juniperus osteosperma*
 - Juniperus scopulorum*
 - Picea engelmannii*
 - Picea pungens*
 - Pinus aristata*
 - Pinus edulis*
 - Pinus flexilis*
 - Pinus ponderosa*
 - Pseudotsuga mensiesii*

- Angiosperms
- Acer glabrum*
 - Acer grandidentatum*
 - Betula occidentalis*
 - Cercocarpus ledifolius*
 - Cercocarpus montanus*
 - Fraxinus anomala*
 - Populus angustifolia*
 - Populus fremontii*
 - Populus tremuloides*
 - Prunus virginiana*
 - Quercus gambelii*
 - Salix bebbiana*
 - Salix scouleriana*
 - Sambucus caerulea*
 - Shepherdia argentea*

Table 3. Bear River Range (Northern Wasatch Mountains), 9,980 ft.

- Gymnosperms
- Abies concolor*
 - Abies lasiocarpa*
 - Juniperus osteosperma*
 - Juniperus scopulorum*
 - Picea engelmannii*
 - Pinus contorta*
 - Pinus flexilis*
 - Pinus monophylla*
 - Pseudotsuga mensiesii*

- Angiosperms
- Acer glabrum*
 - Acer grandidentatum*
 - Acer negundo*
 - Alnus tenuifolia*
 - Betula occidentalis*
 - Cercocarpus ledifolius*
 - Cercocarpus montanus*
 - Crataegus rivularis*
 - Populus angustifolia*
 - Populus tremuloides*
 - Prunus virginiana*
 - Salix amygdaloides*
 - Salix bebbiana*
 - Salix lasiandra*
 - Salix scouleriana*
 - Sambucus caerulea*
 - Sorbus scopulina*

Table 4. Beaver Dam Mountains, 7,746 ft. (Including Beaver Dam Wash), 2,500 ft.

- Gymnosperms
- Abies concolor*
 - Juniperus osteosperma*
 - Juniperus scopulorum*
 - Pinus monophylla*
 - Pinus ponderosa*

- Angiosperms
- Acacia greggii*
 - Acer negundo*
 - Cercis occidentalis*
 - Cercocarpus ledifolius*
 - Cercocarpus montanus*
 - Chilopsis linearis*
 - Fraxinus anomala*
 - Fraxinus velutina*
 - Populus fremontii*
 - Prosopis glandulosa*
 - Prosopis pubescens*
 - Quercus gambelii*
 - Quercus turbinella*
 - Salix bebbiana*
 - Salix laevigata*
 - Yucca brevifolia*

Table 5. Canyonlands National Park, Elev. ca. 3,000-6,000 ft.

- Gymnosperms
- Juniperus osteosperma*
 - Pinus edulis*
 - Pinus ponderosa*

Angiosperms

Acer negundo
Celtis reticulata
Cercocarpus montanus
Fraxinus anomala
Ostrya knowltonii
Populus fremontii
Quercus gambelii
Rhamnus betulaeifolia
Salix amygdaloides
Salix nigra

Table 6. Canyon Mountains, 9,717 ft.

Gymnosperms

Abies concolor
Juniperus osteosperma
Juniperus scopulorum
Pinus edulis
Pinus monophylla
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer grandidentatum
Cercocarpus ledifolius
Cercocarpus montanus
Crataegus rivularis
Populus angustifolia
Prunus virginiana
Quercus gambelii
Salix bebbiana
Salix lasiolepis
Salix scouleriana
Sambucus caerulea

Table 7. Cedar Mountains, 7,039 ft.

no collections

Table 8. Confusion Range, 8,300 ft.

no collections

Table 9. Deep Creek Mountains, 12,101 ft.

Gymnosperms

Abies concolor
*Abies lasiocarpa**
Juniperus osteosperma
Juniperus scopulorum
Picea engelmannii
Picea pungens
*Pinus aristata**
Pinus flexilis
Pinus monophylla
*Pseudotsuga mensiesii**

Angiosperms

Acer glabrum
Betula occidentalis
Cercocarpus ledifolius
*Populus angustifolia**
*Populus tremuloides**
Prunus virginiana
Salix bebbiana
Salix lasiandra
Salix scouleriana
Sambucus caerulea

Table 10. East Tintic Mountains, 8,218 ft.

Gymnosperms

Juniperus osteosperma
Pinus edulis
Pinus monophylla

Angiosperms

Acer grandidentatum

Table 11. Fish Springs Range, 7,680 ft.

no collections

Table 12. Goose Creek Mountains, 8,690 ft.

Gymnosperms

Juniperus osteosperma

Angiosperms

Cercocarpus ledifolius

Table 13. Green River Valley, Uinta Basin, ca. 5,000 ft.

Gymnosperms

Juniperus osteosperma
Juniperus scopulorum
Pinus edulis
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer negundo
Betula occidentalis
Celtis reticulata
Cercocarpus ledifolius
Cercocarpus montanus
Crataegus rivularis
Fraxinus anomala
Populus angustifolia
Populus fremontii
Prunus virginiana
Salix amygdaloides
Sambucus caerulea
Shepherdia argentea

Table 14. Grouse Creek Mountains, 9,042 ft.

Gymnosperms

Juniperus osteosperma
Pinus monophylla

Angiosperms

Betula occidentalis
Populus tremuloides
Prunus virginiana

Table 15. Henry Mountains, 11,615 ft.

Gymnosperms

Abies lasiocarpa
Juniperus osteosperma
Juniperus scopulorum
Pinus aristata
Pinus flexilis

Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Acer negundo
Betula occidentalis
Cercocarpus ledifolius
Cercocarpus montanus
Fraxinus anomala
Populus angustifolia
Populus fremontii
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix bebbiana
Salix lasiandra
Salix scouleriana
Shepherdia argentea

Table 16. House Range, 9,687 ft.

Gymnosperms

Juniperus osteosperma
Pinus monophylla

Table 17. Kaiparowits Plateau, 7,610 ft.

Gymnosperms

Juniperus osteosperma

Angiosperms

Acer grandidentatum
Fraxinus anomala
Quercus gambelii

Table 18. La Sal Mountains, 12,721 ft.

Gymnosperms

Abies concolor
Abies lasiocarpa
Juniperus osteosperma
Picea engelmannii
Pinus edulis
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Acer negundo
Alnus tenuifolia
Betula occidentalis
Cercocarpus montanus
Crataegus rivularis
Fraxinus anomala
Populus angustifolia
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix bebbiana
Salix lasiandra
Salix scouleriana
Sambucus caerulea
Shepherdia argentea
Sorbus scopulina

Table 19. Markagunt Plateau, 11,317 ft. (Excluding Washington Co.)

Gymnosperms

Abies concolor
Abies lasiocarpa
Juniperus scopulorum
Picea engelmannii
Picea pungens
Pinus aristata
Pinus edulis
Pinus flexilis
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Acer grandidentatum
Acer negundo
Betula occidentalis
Cercocarpus ledifolius
Cercocarpus montanus
Fraxinus anomala
Populus fremontii
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix lasiolepis
Sambucus caerulea
Shepherdia argentea

Table 20. Mineral Mountains, 9,619 ft.

Gymnosperms

Pinus edulis

Angiosperms

Prunus virginiana
*Quercus gambelii**
Shepherdia argentea

Table 21. Navajo Mountain, 10,388 ft.

Gymnosperms

Picea pungens
Pinus flexilis
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Cercocarpus ledifolius
Populus tremuloides
Rhamnus betulaeifolia

Table 22. Needle Range, 9,785 ft.

Gymnosperms

Abies concolor
Pinus aristata

Angiosperms

Acer glabrum
Cercocarpus ledifolius
Populus tremuloides
Sambucus caerulea

Table 23. Onaqui Mountains, 9,067 ft.

Gymnosperms

Juniperus osteosperma

Table 24. Oquirrh Mountains, 10,626 ft.

Gymnosperms

Abies concolor
Abies lasiocarpa
Juniperus scopulorum
Pseudotsuga mensiesii

Angiosperms

Cercocarpus ledifolius
Cercocarpus montanus
Populus angustifolia
Populus tremuloides
Prunus virginiana
Quercus gambelii
Sambucus caerulea

Table 25. Pavant Mountains, 10,279 ft.

Gymnosperms

Abies concolor
Juniperus osteosperma
Juniperus scopulorum
Pinus edulis
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Acer grandidentatum
Acer negundo
Betula occidentalis
Celtis reticulata
Cercocarpus ledifolius
Cercocarpus montanus
Crataegus rivularis
Populus angustifolia
Populus fremontii
Prunus virginiana
Quercus gambelii
Salix amygdaloides
Salix lasiandra
Sambucus caerulea
Shepherdia argentea

Table 26. Pilot Range (Utah portion ca. 8,000 ft.)

Gymnosperms

Pinus flexilis

Table 27. Pine Valley Mountains, 10,238 ft. & Upper Santa Clara River Valley ca. 3,500 ft.

Gymnosperms

Abies concolor
*Abies lasiocarpa**
Juniperus osteosperma
Pinus aristata
Pinus flexilis
Pinus monophylla
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Acer grandidentatum
Acer negundo
Betula occidentalis
Celtis reticulata
Cercis occidentalis

Cercocarpus ledifolius
Cercocarpus montanus
Chilopsis linearis
Fraxinus anomala
Fraxinus velutina
Populus angustifolia
Populus fremontii
Populus tremuloides
Prosopis glandulosa
Prosopis pubescens
Prunus virginiana
Quercus gambelii
Quercus tubinella
Rhamnus betulaeifolia
Robinia neomexicana
Salix bebbiana
Salix laevigata
Salix lasiolepis
Salix scouleriana
Sambucus caerulea
Sorbus scopulina

Table 28. Raft River Mountains, 9,829 ft.

Gymnosperms

Abies concolor
Abies lasiocarpa
Juniperus osteosperma
Juniperus scopulorum
Picea engelmannii
Pinus flexilis
Pinus monophylla
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Alnus tenuifolia
Betula occidentalis
Cercocarpus ledifolius
Populus angustifolia
Populus tremuloides
Prunus virginiana
Salix bebbiana
Salix lasiandra
Salix scouleriana
Sambucus caerulea

Table 29. Roan (Tavaputs) Plateau (east), 9,510 ft.

Gymnosperms

Abies concolor
Juniperus osteosperma
Juniperus scopulorum
Picea engelmannii
Pinus edulis
Pinus flexilis
Pinus ponderosa
Pseudotsuga mensiesii

Angiosperms

Acer glabrum
Acer grandidentatum
Celtis reticulata
Cercocarpus ledifolius
Cercocarpus montanus
Fraxinus anomala
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix amygdaloides
Sambucus caerulea

Table 30. Roan (Tavaputs) Plateau (west), 10,235 ft. Angiosperms

Gymnosperms

- Abies concolor*
- Abies lasiocarpa*
- Juniperus osteosperma*
- Juniperus scopulorum*
- Picea engelmannii*
- Picea pungens*
- Pinus aristata*
- Pinus edulis*
- Pinus flexilis*
- Pinus ponderosa*
- Pseudotsuga mensiesii*

Angiosperms

- Acer glabrum*
- Acer grandidentatum*
- Acer negundo*
- Betula occidentalis*
- Cercocarpus ledifolius*
- Cercocarpus montanus*
- Crataegus rivularis*
- Populus angustifolia*
- Populus fremontii*
- Populus tremuloides*
- Prunus virginiana*
- Quercus gambelii*
- Salix amygdaloides*
- Salix bebbiana*
- Salix lasiandra*
- Sambucus caerulea*
- Shepherdia argentea*

Table 31. San Francisco Mountains, 9,669 ft.

Gymnosperms

- Juniperus osteosperma*
- Pinus monophylla*

Angiosperms

- Cercocarpus montanus*

Table 32. San Pitch Mountains, 9,487 ft.

Gymnosperms

- Abies concolor*
- Juniperus osteosperma*
- Juniperus scopulorum*
- Pinus edulis*
- Pseudotsuga mensiesii*

Angiosperms

- Acer glabrum*
- Acer grandidentatum*
- Cercocarpus ledifolius*
- Cercocarpus montanus*
- Crataegus rivularis*
- Populus angustifolia*
- Prunus virginiana*
- Quercus gambelii*
- Sambucus caerulea*
- Sorbus scopulina*

Table 33. San Rafael Swell, 7,921 ft.

Gymnosperms

- Juniperus osteosperma*
- Pinus edulis*
- Pinus ponderosa*

- Betula occidentalis*
- Celtis reticulata*
- Cercocarpus montanus*
- Fraxinus anomala*
- Populus fremontii*
- Shepherdia argentea*

Table 34. Simpson Mountains, 8,450 ft.

no collections

Table 35. Stansbury Mountains, 11,031 ft.

Gymnosperms

- Abies concolor*
- Abies lasiocarpa*
- Juniperus osteosperma*
- Juniperus scopulorum*
- Picea engelmannii*
- Pinus flexilis*
- Pseudotsuga mensiesii*

Angiosperms

- Acer glabrum*
- Acer negundo*
- Cercocarpus ledifolius*
- Populus tremuloides*
- Prunus virginiana*
- Salix scouleriana*

Table 36. Tushar Mountains, 12,173 ft.

Gymnosperms

- Abies concolor*
- Abies lasiocarpa*
- Juniperus osteosperma*
- Juniperus scopulorum*
- Picea pungens*
- Pinus edulis*
- Pinus flexilis*
- Pinus ponderosa*
- Pseudotsuga mensiesii*

Angiosperms

- Acer glabrum*
- Acer grandidentatum*
- Acer negundo*
- Betula occidentalis*
- Cercocarpus montanus*
- Populus angustifolia*
- Populus tremuloides*
- Prunus virginiana*
- Quercus gambelii*
- Salix bebbiana*
- Salix lasiandra*
- Salix scouleriana*
- Sambucus caerulea*
- Shepherdia argentea*

Table 37. Uinta Mountains, 13,498 ft.

Gymnosperms

- Abies concolor*
- Abies lasiocarpa*
- Juniperus osteosperma*
- Juniperus scopulorum*
- Picea engelmannii*
- Picea pungens*
- Pinus contorta*

Pinus edulis
Pinus flexilis
Pinus ponderosa
Pseudotsuga menziesii

Angiosperms

Acer glabrum
Acer grandidentatum
Acer negundo
Alnus tenuifolia
Betula occidentalis
Celtis reticulata
Cercocarpus ledifolius
Cercocarpus montanus
Crataegus rivularis
Populus angustifolia
Populus fremontii
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix amygdaloides
Salix bebbiana
Salix lasiandra
Salix scouleriana
Sambucus caerulea
Shepherdia argentea
Sorbus scopulina

Table 38. Wah Wah Mountains, 9,200 ft.

Gymnosperms

Abies concolor
Juniperus osteosperma
Juniperus scopulorum
Pinus aristata
Pinus monophylla
Pinus ponderosa
Pseudotsuga menziesii

Angiosperms

Acer glabrum
Acer grandidentatum
Cercocarpus ledifolius
Populus tremuloides
Prunus virginiana
Salix bebbiana

Table 39. Wasatch Plateau 11,300 ft.

Gymnosperms

Abies concolor
Abies lasiocarpa
Juniperus osteosperma
Juniperus scopulorum
Picea engelmannii
Picea pungens
Pinus edulis
Pinus flexilis
Pinus ponderosa
Pseudotsuga menziesii

Angiosperms

Acer glabrum
Acer grandidentatum
Acer negundo
Alnus tenuifolia
Betula occidentalis
Cercocarpus ledifolius
Cercocarpus montanus

Crataegus rivularis
Populus angustifolia
Populus fremontii
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix bebbiana
Salix lasiandra
Salix scouleriana
Sambucus caerulea
Shepherdia argentea
Sorbus scopulina

Table 40. Wasatch Range (South of Weber Co.), 11,877 ft.

Gymnosperms

Abies concolor
Abies lasiocarpa
Juniperus osteosperma
Juniperus scopulorum
Picea engelmannii
Picea pungens
Pinus edulis
Pinus flexilis
Pinus ponderosa
Pseudotsuga menziesii

Angiosperms

Acer glabrum
Acer grandidentatum
Acer negundo
Alnus tenuifolia
Betula occidentalis
Celtis reticulata
Cercocarpus ledifolius
Cercocarpus montanus
Crataegus rivularis
Crataegus succulenta
Populus angustifolia
Populus fremontii
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix amygdaloides
Salix bebbiana
Salix lasiandra
Salix scouleriana
Sambucus caerulea
Shepherdia argentea
Sorbus scopulina

Table 41. West Tintic & Sheeprock Mountains, 9,154 ft.

Gymnosperms

Juniperus osteosperma
Pinus edulis
Pinus monophylla
Pseudotsuga menziesii

Angiosperms

Acer glabrum
Cercocarpus ledifolius
Cercocarpus montanus
Populus tremuloides
Prunus virginiana
Quercus gambelii
Salix bebbiana
Salix lasiolepis
Salix scouleriana

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**FLORA OF THE NATIONAL
REACTOR TESTING STATION**

by

N. Duane Atwood



BIOLOGICAL SERIES—VOLUME XI, NUMBER 4

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FLORA OF THE NATIONAL REACTOR TESTING STATION¹

by

N. Duane Atwood²

INTRODUCTION

Statement of Problem

This study of the flora of the National Reactor Testing Station (NRTS) was undertaken because no intensive investigation on plant taxonomy has been

made in this area. This region deserves study because the station contains several unique areas such as the well known Sinks and the Big and Little Lost Rivers which disappear in the Sinks region.

PROCEDURE

Plant collections were begun in the spring of 1967 and continued through September of that year. The author spent all of the collecting season of 1967 on the test site. Additional collecting trips were made during the growing season of 1968.

An attempt was made to collect representatives of all vascular plants within the boundaries of the NRTS. Additional collections were made in areas adjacent to the test site. Some collections not actually made on the site are included in this treatment. Only those plants which grew on habitats similar to those found on the NRTS are included, with two exceptions; (1) all plants collected on Big Southern Butte and (2) those plants along that portion of

Birch Creek just north of the site are included.

Since the Big Lost River is relatively inaccessible along much of its course a trip was made by raft from the western edge of the test site to a point where the river crosses U. S. Highway 20-26.

All pertinent specimens in the herbaria of Idaho State College (IDS), Utah State University (UTC), and the NRTS were examined. All specimens cited in this work are those of the author, unless otherwise indicated, and are deposited in the herbarium of Brigham Young University.

Measurements were made from herbarium specimens using a standard centimeter scale graduated in millimeters.

REVIEW OF THE LITERATURE

The first account of botanical collecting in the general region of the NRTS was that of Wyeth and his party in 1833 (McKelvey, 1955). On June 2nd his journal records:

... through an open plain nearly level finished the streams of Salmon river and struck on called Little Godin it terminates near the three butes in a little lake here goes S.E. through the valley ... the mts. appear terminating on both sides (sic).

(They kept along this valley on the 3rd and 4th and on the 5th.)

Saw the three Butes come in sight one by one and then the Trois Tetons ... the Butes S.E. by S. 20 miles distant about so far this river rapid and little and not beaver grass worse and worse (sic).

While descending the valley of Lost River, Wyeth and his party turned northeastward and traveled

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²Department of Botany, Brigham Young University, Provo, Utah.



Fig. 1. Typical sagebrush-grass community comprized of *Artemisia tridentata*, *Stipa comata*, and *Oryzopsis hymenoides*



Fig. 2. Sinks area looking east.

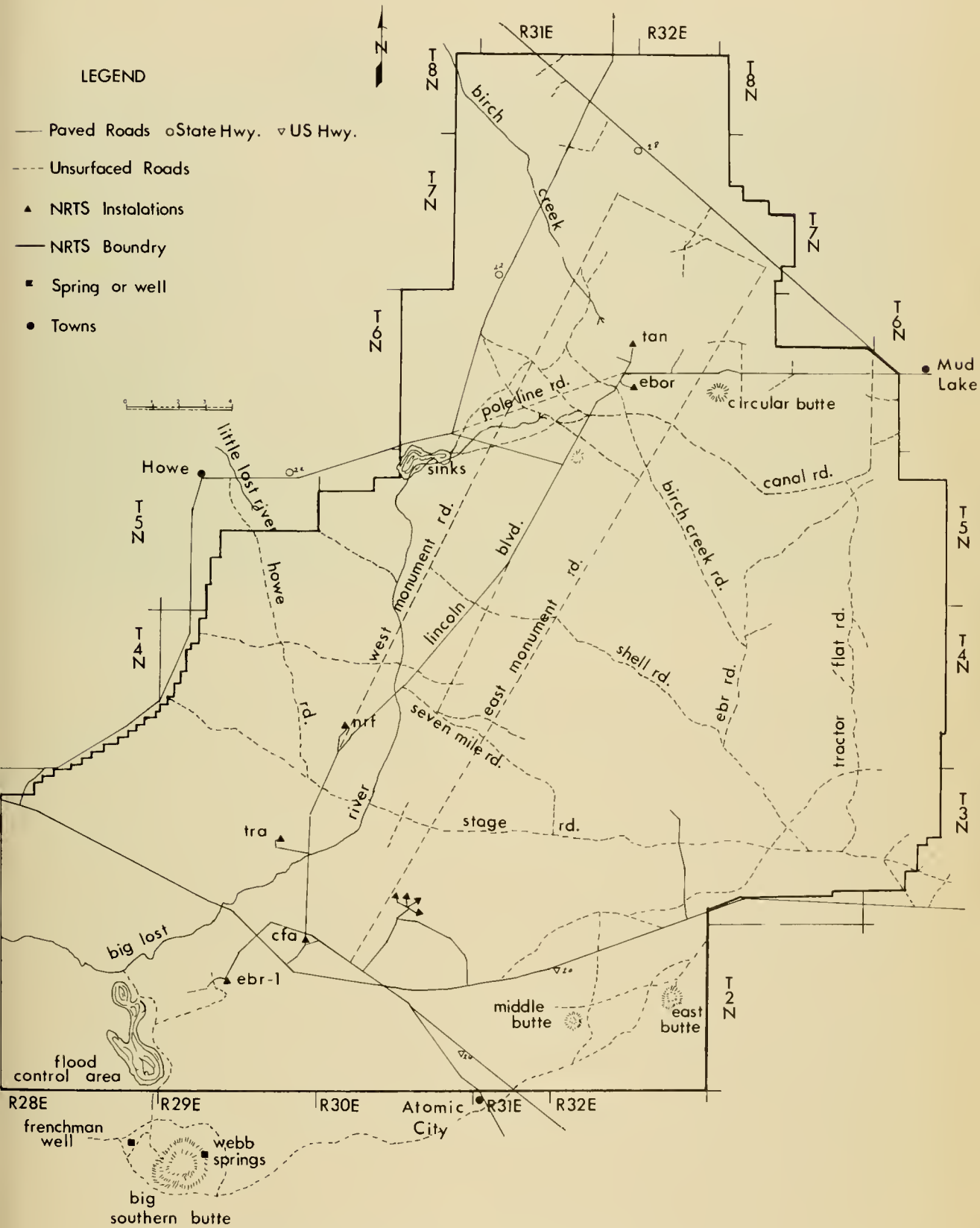


Fig. 3. Principal roads used to make plant collections. Modified from Allred (1968).



Fig. 4. Big Lost River during spring run off.

across the northeastern end of the Snake River Plain (presently the northeastern portion of the NRTS), and camped on the Camas River (June 20-23). From this camp Wyeth penned a number of letters, one to his friend Nuttall in Cambridge, mentioning a package of plants being shipped which, however, never reached its destination.

It is interesting that this is the earliest account of botanical collecting in the intermountain region.

The next collections were those of Nuttall and Townsend in their travels to the Columbia River with Wyeth's second transcontinental expedition.

They were in the area of the Lost River and Camas prairie from August 7th to August 12, 1834.

To my knowledge, Palmer was the next botanist to collect plants in the vicinity of the site and was there around 1893 (Davis, 1968 personal communication and Reveal, 1969 personal communication).

Since 1900 the most important collections have been made by R. J. Davis who collected in this area periodically from the late 20's until about 1952. The Atomic Energy Commission supported workers who made a substantial contribution in 1950 when they collected a series of plants (about 180) during the spring of that year. Many of these are deposited in the herbarium of Idaho State College. Some of these plants are also present in a small collection in the ecology branch of the NRTS.

Geographical description of the National Reactor Testing Station

The National Reactor Testing Station is situated along the western edge of the upper Snake River Plain in southeastern Idaho. Most of the test site lies in the eastern portion of Butte County, at the base of the Lost River, Lehmi, and Beaverhead Mountains; the remainder of the site occupies portions of Bingham, Jefferson, Clark, and Bonneville Counties. The 894 square miles which comprise the station is more or less rolling to broken land, typical of this portion of the Columbia Plateaus Province. The plain is broken by three large buttes, all volcanic in nature. Middle and East Buttes, which are located in the southeastern portion of the test site, rise from the plain at an elevation of 5,200 feet, to elevations of 6,394 feet and 6,605 feet respectively. Big Butte is located just south of the NRTS and towers to an elevation of 7,576 feet.

Little Lost River and Birch and Camas Creeks enter the station from the north and drain into the sinks in the northwestern portion of the site.

Geology

The Snake River Plain was formed by the interbedding of volcanic rocks and of lake and alluvial deposits. The alluvial deposits are quaternary in age

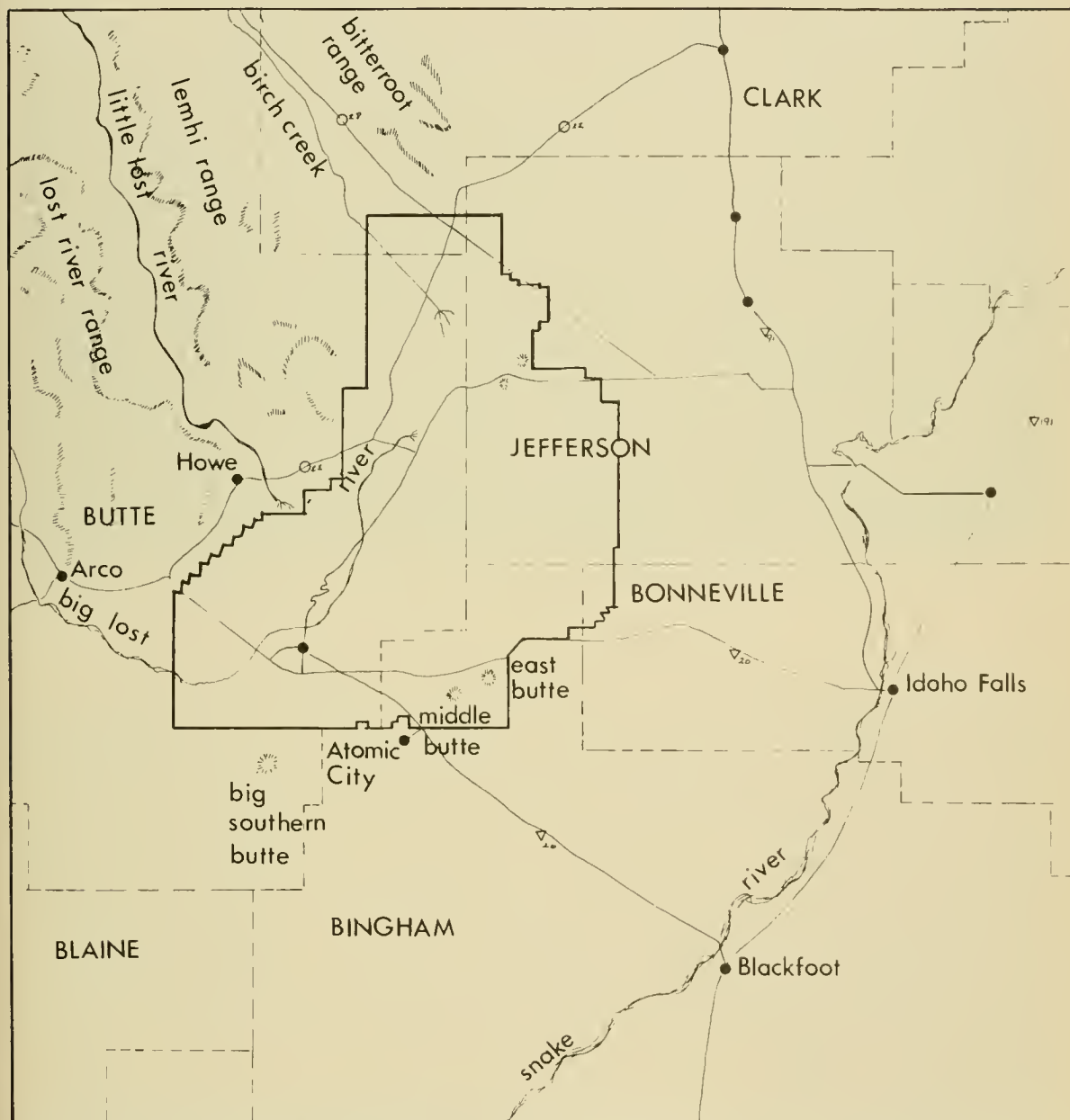


Fig. 5. Location of National Reactor Testing Station in relationship to some cities in southeastern Idaho. Modified from Allred (1968).



Fig. 6. Lemhi Mountains in northwestern portion of National Reactor Testing Station.



Fig. 7. Middle and East Butte with wild rye patch in foreground.

NRTS VEGETATION TYPE MAP

LEGEND

- NRTS Boundry
- Highway
- ~ Intermittent Streams
- Instalations
- ★ Big Sagebrush - Bluebunch Wheatgrass - Rabbitbrush
- ☆ Big Sagebrush - Rabbitbrush - Foxtail
- ⊙ Big Sagebrush - Thickspike Wheatgrass - Needlegrass
- ⊕ Big Sagebrush - Winterfat - Rabbitbrush
- ⊖ Big Sagebrush - Winterfat - Saltbush
- ⊗ Big Sagebrush - Shadscale - Rabbitbrush
- ⊘ Big Sagebrush - Ricegrass - Needlegrass
- ⊙ Black Sagebrush - Big Sagebrush - Shadscale
- ⊖ Small Sagebrush - Shadscale - Foxtail
- ⊗ Crested Wheatgrass (seeded)
- ⊘ Bluebunch Wheatgrass - Threetip Sage - Rabbitbrush
- ⊙ Bluestem Wheatgrass - Wiregrass - Iva
- ★ Ricegrass - Needlegrass - Rabbitbrush - Cactus
- ⊙ Canada Wild Rye - Rabbitbrush - Big Sagebrush
- ⊖ Juniper - Big Sagebrush - Bluebunch Wheatgrass
- ⊙ Horsebrush - Rabbitbrush - Big Sagebrush
- ⊖ Rabbitbrush - Big Sagebrush - Grass
- ⊙ Saltbush - Winterfat - Indian Ricegrass
- ⊖ Mixed Shrub
- ⊙ Sand Dunes

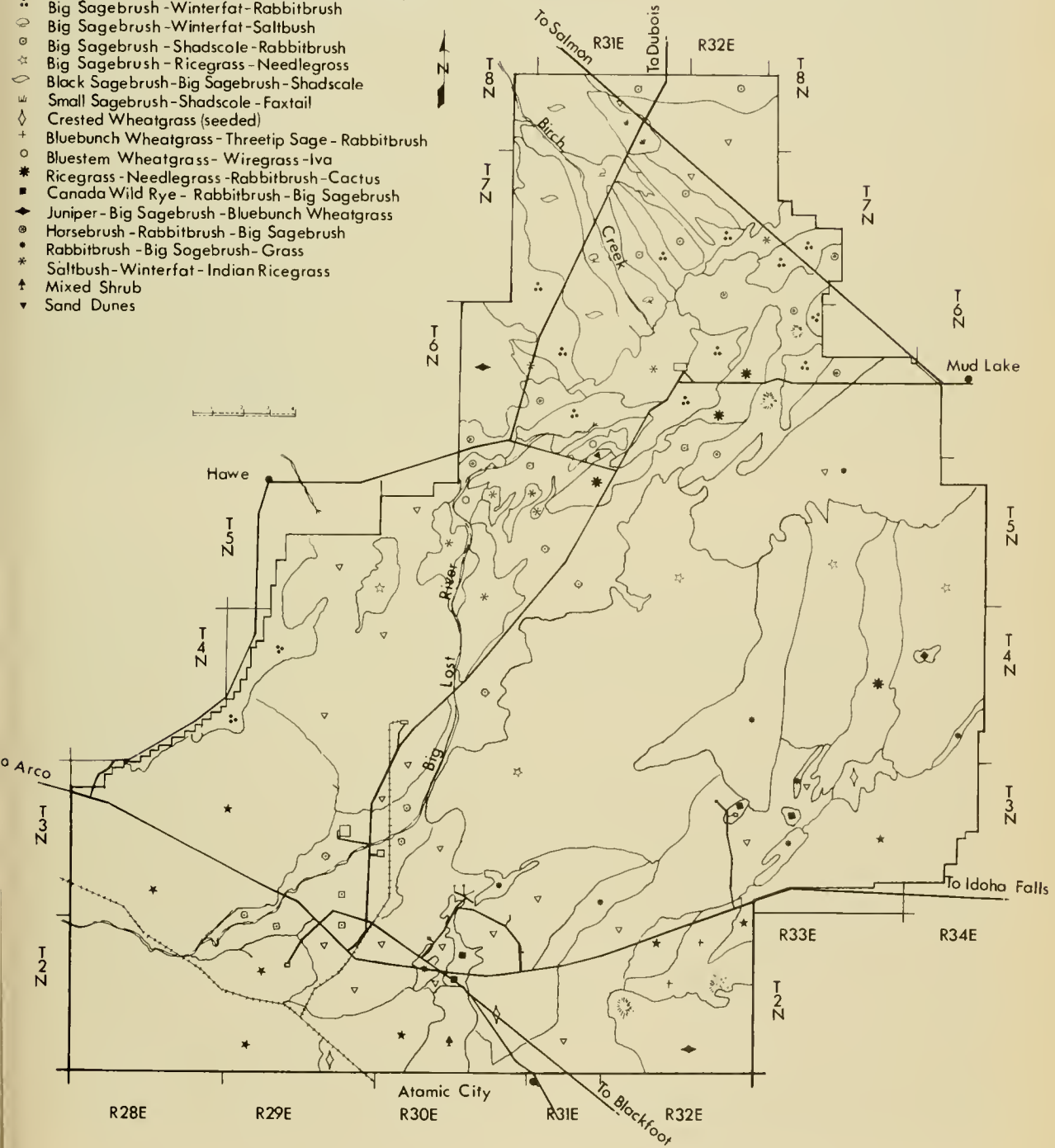


Fig. 8. Major plant communities as designated by McBride. Modified from McBride (1968).

and are present along the streams flowing onto the site. The northern part of the station, south and west of Mud Lake, is covered by lake and eolian deposits; these are mostly of unconsolidated clay, silt, and sand and are represented as far west as the sinks. Exposures of basalt are less common within this area. East, Middle, and Big Butte are probably sources of much of the lava flow. Middle Butte is composed entirely of basalt. Big Butte is mostly rhyolite with some basalt, and East Butte consists of trachyte and rhyolite with some basalt, and East Butte consists of trachyte and rhyolitic rocks. All three Buttes are middle tertiary in age, somewhat older than the quaternary basalt flows surrounding them. Many of the basalt flows are in excess of 1,500 feet in thickness.

Ecology

The NRTS is located at the eastern end of the Snake River Plain in a broad, more or less flat valley. The prevailing air masses pass over the mountain ranges to the west and north before entering the site, and in doing so lose the major portion of their moisture. Annual precipitation at the station is between seven and eight inches. Temperatures vary from 102 degrees F as a high and minus 43 degrees F as a low. The average annual temperature is 42 degrees F. The intense cold common in most of that region east of

the Rocky Mountains does not generally prevail in the Snake River Plain, due to the effective barrier of the Beaverhead and Centennial Mountains.

The vegetation of this semidesert belongs to the northern desert shrub biome. According to French, et al (1965), *Artemisia tridentata* occupies about 80 percent of the site. McBride (1968), in his vegetation map (Fig. 1) of the NRTS, recognized 19 major plant communities. Allred (1968), in his ecological investigations, established study areas in the major vegetation types as outlined by McBride. Detailed plant analysis within Allred's study areas demonstrated some variation from McBride's designations.

Poorly drained, saline soil depressions support various members of the family Chenopodiaceae, such as *Sarcobatus vermiculatus*, *Grayia spinosa*, *Eurotia lanata*, and several *Atriplex* species. *Juniperus osteosperma* is dominant on rocky ridges extending onto the site. Sandy areas, particularly south of Mud Lake, support stands of grasses of which *Oryzopsis hymenoides*, *Stipa comata*, and *Aristida fendleriana* are dominant. Species of *Chrysothamnus* are also an important part of the vegetation in sandy areas. Among the grasses, *Agropyron spicatum* appears to be the most important single species, although *Poa secunda*, *Koeleria cristata*, *Stipa* spp., *Agropyron dasystachyum*, *Oryzopsis hymenoides*, and others, are common. The streams which enter the site support various species of trees, shrubs, grasses and forbs.



Fig. 9. *Oryzopsis hymenoides-Stipa comata* grass community in Tractor Flat on northeast portion of site.



Fig. 10. Stand of juniper along Idaho highway 22, five miles north of junction with Idaho highway 88.



Fig. 11. *Artemisia-Atriplex* community three miles north of Pole Line Road. Lemhi Mountains in background.



Fig. 12. Mixed community of *Chrysothamnus*, grass, *Tetradymia*, and *Opuntia*.



Fig. 13. Sand dunes with Russian thistle in foreground. Located just northwest of junction with Idaho highway 88—Lincoln Blvd.

Arrangement of Plant Families, Genera, and Species

All taxa from division to species are arranged in alphabetical order. The primary purpose of this work is to provide a means of identifying the plants of the National Reactor Testing Station. Keys have been

made for all families, genera, and species. In addition, distribution, phenology, and a voucher specimen citation is given for each of the species.

TAXONOMIC TREATMENT

Key to the Higher Taxa

1. Plants reproducing by seeds; cone or flower bearing plants DIVISION SPERMATOPHYTA (2)
1. Plants without seeds or flowers, reproducing by spores in sporangia; fernlike or rushlike plants DIVISION PTERIDOPHYTA, p. 44
2. Seeds borne in a closed carpel of a flower; stigmas present; plants mostly deciduous ... CLASS ANGIOSPERMAE (3)
2. Seeds borne on the surface of scales or bracts, arranged in cones; stigmas none; plants evergreen trees CLASS GYMNOSPERMAE, p. 43
3. Embryo usually with 1 cotyledon; floral parts usually in threes; leaves mostly parallel veined SUBCLASS MONOCOTYLEDONEAE, p. 39
3. Embryo usually with 2 cotyledons; floral parts commonly in fours or fives; leaves mostly net-veined SUBCLASS DICOTYLEDONEAE (4)
4. Corolla lacking; calyx, when present, with segments much alike, sometimes petaloid ... SERIES APETALAE, p. 11
4. Corolla and calyx present, commonly different in texture and color 5
5. Petals more or less united SERIES GAMOPETALAE, p. 12
5. Petals distinct, at least at the base SERIES POLYPETALAE, p. 12

CLASS ANGIOSPERMAE

SUBCLASS DICOTYLEDONEAE

SERIES APETALAE

1. Plants woody, trees or shrubs 2
1. Plants herbaceous, sometimes woody only at the base 8
2. Flowers borne in catkins SALICACEAE, p. 35
2. Flowers not in catkins, perfect or unisexual 3
3. Flowers several to many, in a head surrounded by an involucre of bracts; calyx wanting; ovary inferior COMPOSITAE, p. 17
3. Flowers 1 to many; calyx usually present 4
4. Ovary inferior; flowers in corymbose or terminal cymes, perfect; stamens usually 5 CORNACEAE, p. 23
4. Ovary superior; trees or shrubs 5
5. Ovary of 1 carpel, with 1 locule, 1 style, 1

- stigma ROSACEAE, p. 34
5. Ovary of 2 or more carpels, several loculed 6
6. Leaves opposite, lobed to compound; fruit a double samara ACERACEAE, p. 14
6. Leaves alternate or opposite, entire to toothed, but not compound; fruit not a double samara, various 7
7. Flowers subtended by a gamophyllous involucre, perfect; stamens mostly 6 to 9; fruit an achene POLYGONACEAE, p. 32
7. Flowers perfect or unisexual, but not subtended by a gamophyllous involucre; stamens 1 to 5, fruit a utricle CHENOPODIACEAE, p. 16
8. Ovary inferior, adnate to the perianth or hypanthium, only appearing fused in Nyctaginaceae 9
8. Ovary superior 12
9. Ovary 2-loculed, 1 ovule in each locule; fruit 2-seeded 10
9. Ovary 1-loculed, 1-2 ovules per locule; fruit 1-seeded 11
10. Perianth parts united; flowers in cymes, not umbellate; leaves opposite or whorled RUBIACEAE, p. 35
10. Perianth parts separate; flowers in umbels; leaves basal or alternate UMBELLIFERAE, p. 38
11. Plants parasitic on the roots of shrubs; perennial herbs with woody base; leaves alternate; flowers greenish white SANTALACEAE, p. 36
11. Plants not parasitic; leaves opposite; inflorescence rarely corymbose; ovules 1 to an ovary NYCTAGINACEAE, p. 30
12. Pistils numerous in a single flower; stamens commonly many RANUNCULACEAE, p. 33
12. Pistils 1 to a flower; stamens 1 to many, usually 10 or less 13
13. Ovary 2 or more loculed; milky juice present EUPHORBIACEAE, p. 26
13. Ovary 1-loculed; plants without milky juice 14
14. Ovary with several to many ovules; fruit a several- to many-seeded capsule; styles 2 to 5; calyx of distinct segments CARYOPHYLLACEAE, p. 15
14. Ovary with a single ovule; fruit a 1-seeded achene or utricle 15
15. Leaves with stipules united to form a sheath around the stem, above the nodes POLYGONACEAE, p. 32
15. Stipules lacking; leaves alternate or opposite 16

- 16. Perianth large, over 5 mm long; style 1, stigma 1; leaves opposite and entire NYCTAGINACEAE, p. 30
- 16. Perianth mostly less than 5 mm long; styles or stigmas more than 1 (usually) 17
- 17. Fruit an achene; plants with stinging hairs URTICACEAE, p. 38
- 17. Fruit a utricle; plants without stinging hairs 18
- 18. Bracts and perianth more or less hyaline or scarious; leaves alternate; plants weedy annuals AMARANTHACEAE, p. 14
- 18. Bracts and perianth herbaceous-fleshy; plants annual or perennial CHENOPODIACEAE, p. 16

SERIES GAMOPETALAE

- 1. Ovary superior 2
- 1. Ovary inferior 15
- 2. Stamens free from the corolla 3
- 2. Stamens at least partially adnate to the corolla 5
- 3. Corolla regular; stamens many, united into a tube (monodelphous); leaves alternate, simple MALVACEAE, p. 29
- 3. Corolla irregular; stamens 4 to 10, diadelphous 4
- 4. Sepals 2, scalelike; petals 4, in 2 sets; leaves finely dissected FUMARIACEAE, p. 26
- 4. Sepals 4 to 5, not scalelike; petals 5, papilionaceous LEGUMINOSAE, p. 27
- 5. Plants devoid of chlorophyll; parasitic on other plants OROBANCHACEAE, p. 30
- 5. Plants with green chlorophyll; plants not parasitic 6
- 6. Ovaries 2, entirely separate below and with a common stigma above; plants with milky juice ASCLEPIADACEAE, p. 14
- 6. Ovary 1; plants without milky juice 7
- 7. Corolla regular or nearly so; stamens mostly 5 (2 or 4) 8
- 7. Corolla irregular 13
- 8. Ovary 4-loculed, 4-lobed, developing into nutlets; inflorescence a scorpioid cyme BORAGINACEAE, p. 14
- 8. OVARY not developing into nutlets; fruit a capsule or berry; 1 to 3-loculed 9
- 9. Ovary 1-loculed; leaves usually alternate 10
- 9. Ovary with 2 or more locules 11
- 10. Corolla dry-scarious, veinless; scapose herbs; sepals and petals 4; stamens 2 or 4; flowers in bracteate spikes or heads PLANTAGINACEAE, p. 31
- 10. Corolla not as above; plants commonly leafy stemmed; perianth 5-merous (in ours); stamens 5 HYDROPHYLLACEAE, p. 26

- 11. Style 3-cleft; ovary 3-loculed POLEMONIACEAE, p. 31
- 11. Style 2-cleft; ovary commonly 2-loculed 12
- 12. Stems trailing or twining CONVOVULACEAE, p. 23
- 12. Stems not trailing or twining; style 1; stigma 1, entire or 2-lobed; fruit a capsule or berry SOLANACEAE, p. 38
- 13. Fruit of 2 to 4 nutlets; leaves opposite 14
- 13. Fruit a capsule; ovary 2-loculed; leaves mostly opposite; corolla sometimes almost regular SCROPHULARIACEAE, p. 36
- 14. Ovary 4-lobed; style arising in the center between the lobes LABIATAE, p. 27
- 14. Ovary not 4-lobed; style apical VERBENACEAE, p. 38
- 15. Stamens numerous; anther sacs opening by slits; petals numerous; plants spiny and succulent CACTACEAE, p. 15
- 15. Stamens 5 or less and not with the above combination of characters 16
- Stamens distinct; leaves whorled or opposite 17
- 16. Stamens united by their anthers into a ring or tube around the style; flowers in involucreal heads COMPOSITAE, p. 17
- 17. Fruit 2-lobed, 2-loculed, separating into 2 one-seeded nutlets; leaves more or less whorled RUBIACEAE, p. 35
- Ovary 2 to 5-loculed; fruit a berrylike drupe; ours shrubs CAPRIFOLIACEAE, p. 15

SERIES POLYPETALAE

- 1. Ovary inferior 2
- 1. Ovary completely superior 13
- 2. Petals many; stems thick and succulent, spiny CACTACEAE, p. 15
- 2. Petals less than 10; stems not succulent or only slightly so, not spiny (see also Rosaceae) 3
- 3. Stamens as many as the petals and opposite them; plants shrubby with thick, leathery leaves RHAMNACEAE, p. 34
- 3. Stamens fewer or more than the petals, or if the same number than alternate with them 4
- 4. Plants woody, trees and shrubs 5
- 4. Plants herbaceous or woody at the base 8
- 5. Fruit a 1- to 2-seeded drupe; flowers many in a flat-topped cyme CORNACEAE, p. 23
- 5. Fruit not a drupe, various, 3 or more seeded; flowers in racemes or corymbs 6
- 6. Leaves opposite; fruit a capsule SAXIFRAGACEAE, p. 36
- 6. Leaves alternate; fruit a pome or berry 7
- 7. Fruit a pome; leaves pinnately veined, lobed or compound; petals commonly much

- larger than the petals ROSACEAE, p. 34
7. Fruit a berry; leaves palmately veined; simple; calyx larger and usually more showy than the petals . . GROSSULARIACEAE, p. 26
8. Stamens 10, 11 or more; plants rough-hairy; fruit a capsule LOASACEAE, p. 29
8. Stamens 10 or fewer; plants not rough-hairy; fruit various 9
9. Ovules and seeds more than 1 in each locule; ovary 1 to 4-loculed 10
9. Ovules and seeds 1 to each locule; ovary 2 to 6-loculed 11
10. Style 1; stamens 4 or 8 ONAGRACEAE, p. 30
10. Styles 2 or more; stamens as many as the petals, twice as many or numerous SAXIFRAGACEAE, p. 36
11. Leaves verticillate, entire; ovary commonly 2-loculed; style 1 CORNACEAE, p. 23
11. Leaves never verticillate; ovary 4 or 2-loculed and then with 2 styles present 12
12. Stamens 2, 4, or 8; petals 2 or 4-merous; style 1; ovary 4-loculed ONAGRACEAE, p. 30
12. Stamens 5; petals 5-merous (rarely 4); ovary with 2 or more styles, 2-loculed; fruit dry, 2-seeded UMBELLIFERAE, p. 38
13. Corolla definitely irregular 14
13. Corolla regular or nearly so 20
14. Leaves variously compound 15
14. Leaves simple, entire to lobed or pinnatifid, not compound 18
15. Petals smaller than the sepals; stamens numerous; ovaries commonly 2 or more or if carpels these united at the base RANUNCULACEAE, p. 33
15. Stamens less than 14; petals as large or larger than the sepals; ovary 1, if merely carpelate then these completely united 16
16. Stamens 6; calyx segments 2 or 4; corolla not papilionaceous 17
16. Stamens commonly 10; calyx of 5 usually united sepals; corolla mostly papilionaceous LEGUMINOSAE, p. 27
17. Sepals 2; corolla spurred FUMARIACEAE, p. 26
17. Sepals 4; corolla not spurred CAPPARIDACEAE, p. 15
18. Stamens many; leaves palmately cleft or parted; carpels commonly more than 1; fruit a follicle RANUNCULACEAE, p. 33
18. Stamens 10 or less; fruit a capsule or legume; leaves simple to compound, but not palmately cleft 19
19. Stamens 5; ovary 1-loculed with 3 placentae; lower petal saccate at the base or spurred VIOLACEAE, p. 39
19. Stamens 10; petals longer than the sepals; fruit a legume LEGUMINOSAE, p. 27
20. Stamens the same number as the petals and opposite them 21
20. Stamens fewer or more than the petals, or if the same number then alternate with them 22
21. Leaves simple and pinnately veined, not lobed, alternate; petals 5, hooded and clawed RHAMNACEAE, p. 34
21. Leaves palmately veined and lobed, opposite; petals 4 or 5, not hooded and clawed ACERACEAE, p. 14
22. Ovary 1, 1-loculed, at least above 23
22. Ovary more than 1, or if 1 then 2 or more loculed 25
23. Ovary simple; style 1; stigma 1; placenta 1 24
23. Ovary compound with more than 1 placenta, style or stigma; plants woody shrubs; leaves alternate ANACARDIACEAE, p. 14
24. Stamens and petals inserted on the calyx tube; leaves various, but not bipinnate ROSACEAE, p. 34
24. Stamens and petals not inserted on the calyx tube; leaves commonly bipinnate LEGUMINOSAE, p. 27
25. Stamens numerous, more than 12 26
25. Stamens not numerous, 12 or less 28
26. Stamens monodelphous MALVACEAE, p. 29
26. Stamens distinct or in several sets 27
27. Stamens and petals inserted on the calyx tube; flowers perigynous ROSACEAE, p. 34
27. Stamens and petals inserted on the receptacle; flowers hypogynous RANUNCULACEAE, p. 33
28. Ovaries 2, united at the tips by a discoid stigma head; plants with milky juice ASCLEPIADACEAE, p. 14
28. Ovaries 1 to many, if united then only at the base; juice rarely milky, if so then not with the foregoing characters 29
29. Ovaries more than 1, separate or united at the base, each with a style 30
29. Ovary 1; style 1 per ovary 31
30. Leaves fleshy, entire; carpels 3 to 5 CRASSULACEAE, p. 23
30. Leaves not fleshy; carpels 2 SAXIFRAGACEAE, p. 36
31. Ovules 1 to 2 in each cell 32
31. Ovules more than 2 in each cell 35
32. Flowers imperfect, borne in calyx-like involucre; plants with milky juice EUPHORBIACEAE, p. 26
32. Flowers perfect, not borne in calyx-like involucre; plants without milky juice . . . 33

- 33. Perianth 4-merous; stamens 6 (4+2)
..... CRUCIFERAE, p. 23
- 33. Perianth 5-merous; stamens 5 or 10 34
- 34. Stamens 5; leaves alternate .. LINACEAE, p. 29
- 34. Stamens 10; leaves commonly opposite
..... GERANIACEAE, p. 26
- 35. Styles 2, distinct; ovary 2-celled; fruit a cap-
sule or berry SAXIFRAGACEAE, p. 36
- 35. Style 1, distinct; ovary 2-celled; fruit a silicle
or silique CRUCIFERAE, p. 23

ACERACEAE. MAPLE FAMILY

1. *Acer* L. Maple

1. *Acer glabrum* Torr. Commonly of the moun-
tains, April to June. Idaho, west from Alaska to Cal-
ifornia, east from Alberta to New Mexico and Ne-
braska. Webb Springs, Butte Co., 26 May 1967, 874.

AMARANTHACEAE. AMARANTH FAMILY

1. *Amaranthus* L. Pigweed; Amaranth

1. *Amaranthus hybridus* L. A weed of waste
places and cultivated ground. Widely distributed
throughout most of North America, June to Novem-
ber. T.6N., R.31E., Butte Co., 29 July 1967, 1182.

ANACARDIACEAE. SUMAC FAMILY

1. *Rhus* L. Sumac

1. *Rhus trilobata* Nutt. Common along streams
and dry hills, May to July. North Dakota to Washing-
ton, south to Texas and California. Big Lost River,
Butte Co., 1 July 1967, 1093.

ASCLEPIADACEAE. MILKWEED FAMILY

1. *Asclepias* L. Milkweed

1. *Asclepias speciosa* Torr. Common over much of
the western and central states, June to August. South
of junction 88—Lincoln Blvd., Butte Co., 24 August
1967, 1209.

BETULACEAE. BIRCH FAMILY

1. *Betula* L. Birch

1. *Betula occidentalis* Hook. Along streams of the
plains and mountains. Utah, west to northern Cal-
ifornia, less frequent to southern British Columbia
and south central Idaho. Birch Creek, Clark Co., 25
June 1967, 1053.

BORGINACEAE. BORAGE FAMILY

- 1. Prostrate annuals; style deeply 2-cleft3. *Coldenia*
- 1. Plants mostly erect or the style entire or shallowly
lobed 2
- 2. Nutlets with prickles on the margins, attached at
or below the middle 3
- 2. Nutlets without prickles 4
- 3. Annual plants; pedicles erect; style longer than the
nutlets 6. *Lappula*
- 3. Plants perennial; pedicles reflexed; styles com-

- monly shorter than the nutlets 5. *Hackelia*
- 4. Calyx enlarged in fruit, veiny, folded, and flat-
tened; stems procumbent 2. *Asperugo*
- 4. Plants not as above 5
- 5. Flowers blue or reddish in bud; nutlets obliquely
attached 8. *Mertensia*
- 5. Flowers other than blue 6
- 6. Stigmas 2; nutlets broadly attached at the base to
a flat receptacle 7. *Lithospermum*
- 6. Stigmas solitary; nutlets attached a little above the
base 7
- 7. Corolla white (ours); fornices present in the throat
and the throat almost closed by them
.....4. *Cryptantha*
- 7. Corolla yellow or orange; fornices wanting and the
throat open 1. *Amsinckia*

1. *Amsinckia* Lehm. Fiddle-neck

1. *Amsinckia menziesii* (Lehm.) N. & M. In culti-
vated fields in dry or moist places, May to September.
Idaho to British Columbia, south to California, and
Nevada. R.29E., T.5N., Butte Co., 25 June 1967,
957. Birch Creek, Clark Co., 25 June 1967; 1049.

2. *Asperugo* L. Madwort

1. *Asperugo procumbens* L. A weedy plant of
fields and waste places, May to July. Over much of
North America; Eurasia. R.29E., T.5N., Butte Co., 12
June 1967, 958.

3. *Coldenia* L.

1. *Coldenia nuttallii* Hook. Sandy soil of the
plains, May to August. Idaho, west from Washington
to California, east to Wyoming, south to Arizona.
Tractor Flat; Jefferson Co., 22 July 1967, 1199.
R.31E., T.6N., Butte Co., 18 July, 1967, 1166.

4. *Cryptantha* Lehm.

- 1. Plants annual 3
- 1. Plants perennial 2
- 2. Leaves strongly ciliate margined, setose; nutlets
ovate, muricate or short rugose, the scar open
and triangular 3. *C. humilis*
- 2. Leaves not strongly ciliate margined, setose and
subtomentose or tomentose; nutlets lanceolate,
rugose, the scar closed or subulate
.....5. *C. spiculifera*
- 3. Calyx circumscissile, plants low mat forming;
flowers solitary in the upper axils
.....1. *C. circumscissa*
- 3. Calyx not circumscissile; plants erect, not form-
ing mats; inflorescence spikelike 4
- 4. Nutlets heteromorphous, three of them tuberu-
late, the others smooth, 1.8-2.3 mm long
.....4. *C. kelseyana*
- 4. Nutlets homomorphous, all smooth, lanceolate,
1.5-2 mm long 5
- 5. Margins of the nutlets prominent and sharply an-
gled, at least above; fruiting calyx 2-4.5 mm long;

corolla 1 to 2 mm wide 6. *C. watsonii*
 5. Margins of the nutlets obtuse or rounded; fruiting calyx 4 to 6 mm long; corolla about 1 mm wide 2. *C. fendleri*

1. *Cryptantha circumscissa* (H. & A.) Johnst. Dry, sandy soil, April to July. Washington to California, east through the Snake River Plains of Idaho, south to Utah, Arizona; Chile and Argentina. R.34E., T.5N., Jefferson Co., 20 June 1967, 1005.

2. *Cryptantha fendleri* (Gray) Greene. Mostly in sandy soil, May to July. Saskatchewan to Washington, east and south to Idaho to Nebraska, Nevada and New Mexico. Tractor Flat, Jefferson Co., 22 July 1967, 1195.

3. *Cryptantha humilis* (Greene) Pays. var. *shantzii* (Tidestr.) Higgins. Idaho, south to Colorado, west to Utah to California. T.4N., R.28E., Butte Co., 798.

4. *Cryptantha kelseyana* Greene Dry, sandy soil of the plains, June to July. Saskatchewan and Montana, south to Idaho and Utah. Tractor Flat, Jefferson Co., 20 June 1967, 991.

5. *Cryptantha spiculifera* Pays. Foothills to the plains, May to July. Idaho, west to Washington and Oregon, north to Montana and Saskatchewan. East of Arco, Butte Co., 17 May 1936, Twitchell and Shaw, s.n. (IDS). East of Arco, 22 June 1939, Davis, 937 (IDS).

6. *Cryptantha watsonii* (Gray) Greene. Foothills and lower valleys, May to August. Western Montana to central Washington, south to Nevada and Colorado. Big Butte, Butte Co., 22 June 1950, AEC, 91 (IDS).

5. *Hackelia* Opiz. Stickseed

1. Corolla limb blue; stems spreading-hirsute at least above; cauline leaves well developed; fornicies minutely papillate 1. *H. jessicae*

1. Corolla limb white to ochroleucous, usually marked with light blue; stems with appressed pubescence above; cauline leaves evidently smaller; fornicies villous-puberulent 2. *H. patens*

1. *Hackelia jessicae* (McGregor) Brand From open slopes to meadowlands, June to August. Alberta to California, south through Montana to Idaho, Wyoming and Utah. Webb Springs, Butte Co., 1 July 1967, 1082.

2. *Hackelia patens* (Nutt.) Johnst. Sagebrush plains to higher elevations in the mountains, June to August. Montana, west to Idaho, south to Wyoming, Utah and Nevada. Northeast of Howe, Butte Co., 10 June 1967, 927.

6. *Lappula* Gilib. Stickseed

1. Nutlets with the marginal prickles in 1 row; corolla limb up to 4 mm wide 2. *L. redowskii*

1. Nutlets with the marginal prickles in 2 rows; corolla limb up to 4 mm wide 1. *L. echinata*

1. *Lappula echinata* Gilib. Mostly weedy plants of waste places, roadsides, and cultivated ground, June to August. Birch Creek, Clark Co., 25 June 1967, 1046. R.29E., T.6N., Butte Co., 10 June 1967, 941. R.34E., T.5N., Jefferson Co., 20 June 1967, 990.

2. *Lappula redowskii* (Hornem.) Greene. Weedy plants, May to July. Common in western North America; Eurasia. T.4N., R.31E., Butte Co., 20 May 1967, 782.

7. *Lithospermum* L. Gromwell

1. *Lithospermum ruderale* Lehm. Dry or quite moist areas in the plains and foothills, April to June. Alberta and British Columbia to California and Colorado. Webb Springs, Butte Co., 24 May 1967, 843.

8. *Mertensia* Roth. Bluebells

1. *Mertensia oblongifolia* (Nutt.) G. Don Sagebrush plains to open slopes, April to July. Montana, south to Utah and Nevada. East Butte, Bingham Co., 18 May 1967, 772.

CACTACEAE. CACTUS FAMILY

1. *Opuntia* Mill. Prickly-pear; Cactus

1. *Opuntia polyacantha* Haw. In sagebrush flats, May to June. British Columbia to Alberta, south to Oregon, Arizona to Texas. Webb Springs; Butte Co., 1 July 1967, 1091a.

CAPPARIDACEAE. CAPER FAMILY

1. *Cleome* L. Bee Plant

1. *Cleome lutea* Hook. In desert plains, usually in sandy soil, May to July. Washington to California, east to Montana, Nebraska and Texas. T.6N., R.30E., Butte Co., 6 June 1967, 898.

CAPRIFOLIACEAE. HONEYSUCKLE FAMILY

1. *Symphoricarpus* DuRoi. Snowberry

1. Corolla 7 to 10 mm long, long and narrow; fruits 7 to 10 mm long 2. *S. oreophilus*

1. Corolla 5 to 7 mm long, short and broad; fruits 10 to 15 mm long 1. *S. albus*

1. *Symphoricarpus albus* (L.) Blake. Open slopes of the plains to wooded areas in the mountains, May to August. Alaska to Quebec, south to California, central Idaho, and Nebraska. East Butte, Bingham Co., 22 June 1967, 1022.

2. *Symphoricarpus oreophilus* Gray. Open ground in the foothills to well up into the mountains, June to August. British Columbia to California, New Mexico. R.30E., T.6N., Butte Co., 11 June 1967, 961.

CARYOPHYLLACEAE. PINK FAMILY

1. *Arenaria* L. Sandwort

1. Inflorescence congested to glomerate; glandular pubescent, at least above 2

1. Inflorescence not congested; plants not glandular 3. *A. kingii*

2. Flowering stems usually less than 10 cm tall, leafy; sepals 5 to 12 mm long: . . . 2. *A. franklinii*
2. Flowering stems taller, from 15 to 50 cm high, nearly leafless; sepals 3 to 6 mm long 1. *A. congesta*
1. *Arenaria congesta* Nutt. var. *lithophila* Rydb. Plains and mountains, June to August. Montana to Washington, Colorado, and California. Big Butte, Butte Co., 1 July 1967, 1107.
2. *Arenaria franklinii* Dougl. var. *franklinii*. Sandy plains and sagebrush slopes, May to June. Central Idaho to central Washington and eastern Oregon and northern Nevada. R.28E., T.4N., Butte Co., 21 May 1967, 807.
3. *Arenaria kingii* (Wats.) Jones var. *glabrescens* (Wats.) Maguire. Dry ridges to alpine slopes, June to August. East central California, southeastern Oregon, east to central Idaho in Custer, Lemhi and Butte Counties. R.31E., T.6N., 9 June 1967, 918.

CHENOPODIACEAE. GOOSEFOOT FAMILY

1. Leaves and bracts spinulose at the tips; fruiting calyx with a broad, transverse wing 8. *Salsola*
1. Leaves and bracts not spinulose 2
2. Spiny shrubs; leaves linear, semiterete; endosperm lacking; embryo spirally coiled . . . 9. *Sarcobatus*
2. Plants herbs or nonspiny shrubs, if spinose then with flattened leaves and the embryo annular; endosperm present 3
3. Flowers imperfect; perianth lacking in the pistillate flowers; plants more or less shrubby (in ours) 4
3. Flowers perfect or polygamous; perianth present; on all flowers, often small; plants mostly herbs 6
4. Bracts dorsally compressed; pubescence mainly of inflated hairs which become scurfy when dry 1. *Atriplex*
4. Bracts laterally compressed; pubescence of branched hairs not inflated 5
5. Fruiting bracts densely long-villous; leaves narrow with revolute margins 4. *Eurotia*
5. Fruiting bracts glabrous; leaves entire, not revolute 5. *Grayia*
6. Stamens usually over 3; perianth enclosing the fruit and more or less concealing it 7
6. Stamens 1; perianth small, fruit exposed 7. *Monolepis*
7. Flowers solitary in the axils of leaves or bracts; each calyx segment with a hooked spine when mature 2. *Bassia*
7. Flowers variously disposed in glomerules; calyx segments without hooked spines 8
8. Leaves tipped with a bristlelike hair, fleshy; flowers in small axillary glomerules 6. *Halogeton*
8. Leaves without a bristlelike hair, not fleshy; flowers usually borne in terminal or axillary glomerules 3. *Chenopodium*

1. *Atriplex* L. Saltbrush; Shadscale

1. Plants annual; monoecious 4. *A. rosea*
1. Plants perennial shrubs; dioecious 2
2. Fruiting bracts 4-winged; leaves sessile or nearly so 1. *A. canescens*
2. Fruiting bracts not winged; leaves petioled . . . 3
3. Plants woody throughout, sharply spinose; mostly 4 to 8 dm tall 2. *A. confertifolia*
3. Plants woody only at the base, not spinose; low spreading plants, mostly 1 to 5 dm tall 3. *A. falcata*
1. *Atriplex canescens* (Pursh) Nutt. var. *canescens* Mostly on saline soils, June to August. Eastern Washington and Oregon, to adjacent California, east to Alberta, South Dakota, Kansas, Texas and Mexico. Big Lost River Bridge, Butte Co., 6 June 1967, 895.
2. *Atriplex confertifolia* (Torr.) Wats. Dry fairly saline soil, June to July. North Dakota to eastern Oregon, south to northern Arizona and California. R.31E., T.6N., Butte Co., 8 June 1967, 1118.
3. *Atriplex falcata* (M.E. Jones) Standl. Usually on concentrated saline soil, June to August. Saskatchewan to Alberta, south to Colorado, Utah, New Mexico, California, north to Washington. Pole Line Road, Butte Co., 11 July 1967, 1133. Snake River Plains, Butte Co., 9 August 1950, R. J. Davis; 63 (IDS).
4. *Atriplex rosea* L. Along roadsides and waste areas, July to September. Much of temperate North America; Old World. Five mi west of Big Butte, Butte Co., 27 July 1950; Davis, 145 (IDS).

2. *Bassia* Allion

1. *Bassia hyssopifolia* (Pall.) Kuntze. Saline soil and irrigated land, July to September. British Columbia to California, east to Nevada, Idaho, and Montana; Asia; sporadic in the eastern United States. Snake River Plains, Butte Co., 9 August 1950, Davis s.n. (IDS).

3. *Chenopodium* L. Lamb's Quarters; Pigweed

1. Leaves narrowly linear to linear, entire, 1-nerved; plants densely farinose 3. *C. leptophyllum*
1. Leaves broader; plants only sparsely farinose to grayish-farinose and greenish above 2
2. Leaves 2 to 4 times longer than wide; pericarp usually adherent to the seed 1. *C. album*
2. Leaves wider, nearly as broad as long; pericarp not tightly adherent to the seed . 2. *C. fremontii*
1. *Chenopodium album* L. Plants weedy, mostly in waste places, June to September. Eurasia; over much of North America. Big Butte, Butte Co., 27 June 1950; Davis 130 (IDS).
2. *Chenopodium fremontii* Wats. From saline soil depressions to sagebrush flats and pine woodlands, June to September.
1. Leaves lanceolate, mostly entire; sparsely farinose 1. var. *atrovirens*

1. Leaves mostly triangular and hastately-lobed; grayish-farinose at least below, greenish above 2. var. *fremontii*
- 2a. *Chenopodium fremontii* Wats. var. *atrovirens* (Rydb.) Fosberg. British Columbia to Alberta, south to Iowa and Colorado, west to Oregon, Nevada, and California. By EBR. II Reactor, Butte Co., 3 July 1967, 1112.
- 2b. *Chenopodium fremontii* Wats. var. *fremontii*. British Columbia, Alberta, south to Texas, Mexico and southern California. Big Lost River, Butte Co., 13 July 1967, 1140.
3. *Chenopodium leptophyllum* Nutt. var. *subglabrum* Wats. Dry soils of the plains and foothills, May to August, Manitoba, Alberta, and Oregon, south to Texas and California. South of Big Butte, Butte Co., 27 June 1950, Davis 150 (IDS).

4. *Eurotia* Adans. Winter Fat

1. *Eurotia lanata* (Pursh) Moq. In saline or alkaline soil of the plains and foothills, May to July in our area. Saskatchewan to Washington, south to Texas and California. T.6N., R.32E., Jefferson Co., 28 July 1967, 1177. Butte Co., 1950, AEC 174 (IDS).

5. *Grayia* H. & A. Hopsage

1. *Grayia spinosa* (Hook.) Moq. Saline soil and dry plains and slopes, April to June, Wyoming to Washington, south to Arizona and California. Cinder Butte, Butte Co., 18 May 1967, 762. Base of Big Butte; Butte Co., 22 June 1950; AEC 96 (IDS).

6. *Halogeton* C. A. Meyer

1. *Halogeton glomeratus* C. A. Meyer. Roadsides and waste ground, July to September. Idaho, Utah, Nevada and California, spreading rapidly. Junction of Highway 88—Lincoln Blvd., Butte Co., 20 June 1967, 1185.

7. *Monolepis* Schrad. Poverty weed

1. *Monolepis nuttalliana* (Schultes) Greene Dry or moist, often saline soil, deserts to middle elevations, May to July. Alberta to Washington, south to Texas and California. Big Butte, Butte Co., 20 June 1950, AEC 14 (IDS). T.2N., R.30E., Butte Co., 13 July 1967, 1135.

8. *Salsola* L. Russian thistle

1. *Salsola kali* L. In moist arid regions of the world, a noxious weed, June to August. Eurasia; throughout most of the western United States, occasionally eastward. T.6N., R.31E., Butte Co., 29 July 1967, 1183.

9. *Sarcobatus* Nees. Greasewood

1. *Sarcobatus vermiculatus* (Hook.) Torr. On saline or alkaline soil in dry regions, May to July. Alberta to Washington, south to New Mexico and

California. Pole Line Road, Butte Co., 26 July 1967. 1176.

COMPOSITAE. COMPOSITE FAMILY

1. Flowers all ligulate and perfect; plants with milky juice GROUP A
1. Flowers not all ligulate; ray flowers, when present, marginal and ligulate; juice watery 2
2. Heads radiate 3
2. Heads discoid or disciform 5
3. Rays white to pink, purple or blue GROUP D
3. Rays yellow or orange, sometimes purple or reddish brown at the base 4
4. Pappus chaffy, or of firm awns, or none; receptacle chaffy, bristly or naked GROUP B
4. Pappus partly or wholly of capillary bristles, sometimes plumose; receptacle naked GROUP C
5. Pappus of many capillary bristles, sometimes plumose GROUP E
5. Pappus of scales, or awns, or very short chaffy bristles or a mere crown, or lacking, not plumose GROUP F

Group A. Flowers all ligulate and perfect; juice milky

1. Pappus of plumose bristles, at least in part 2
1. Pappus none, of scales or simple bristles, not plumose 3
2. Achenes beaked at the tip; involucre 2 cm long or more; leaves entire, large 34. *Tragopogon*
2. Achenes not beaked, involucre less than 2 cm long; leaves small and often scalelike 30. *Stephanomeria*
3. Achenes more or less flattened; stems leafy; heads in panicles or umbels; achenes beaked 23. *Lactuca*
3. Achenes not flattened; stems leafy or scapose; heads solitary to many 4
4. Flowers pink or purple; leaves linear, subulate or reduced 24. *Lygodesmia*
4. Rays yellow, sometimes drying to pink; leaves larger, entire to pinnatifid 5
5. Heads several or numerous, rarely solitary 13. *Crepis*
5. Heads 1 per scape or stem 6
6. Achenes 8 to 10-ribbed or nerved, not spinulose-mucronate; involucre bracts imbricated in several series 2. *Agoseris*
6. Achenes 4 to 5-ribbed, spinulose-mucronate, principal bracts of the involucre in 1 series 31. *Taraxacum*

Group B. Rays yellow; pappus chaffy, or of firm awns, or none.

1. Receptacle chaffy or bristly throughout 2

- 1. Receptacle naked 3
- 2. Rays neutral; style branches flattened; pappus of 2 readily deciduous awns; leaves mostly basal forming rosettes, cauline leaves reduced 7. *Balsamorhiza*
- 2. Rays pistillate and fertile; style branches slender; pappus wanting; leaves mostly cauline 20. *Helianthus*
- 3. Rays short and inconspicuous, 1 to 5 mm long; heads smaller, less than 5 mm wide 18. *Gutierrezia*
- 3. Rays well developed, 5 to 30 mm long; heads 5 mm or more wide 4
- 4. Pappus of firm deciduous awns; involucre strongly resinous 17. *Grindelia*
- 4. Pappus of chaffy scales; involucre tomentose 15. *Eriophyllum*

Group C. Rays yellow; pappus partly or wholly of capillary bristles.

- 1. Plants compact dwarf shrubs ..19. *Haplopappus*
- 1. Herbaceous plants 2
- 2. Rays white, pink, purple, or violet 3
- 2. Rays yellow or orange 4
- 3. Style tips deltoid, obtuse or rounded; phyllaries usually equal or little graded; rays narrow 14. *Erigeron*
- 3. Style tips lanceolate or narrower; phyllaries either subequal and the outer leafy, or usually imbricate; leaves alternate and spinulose-toothed 25. *Machaeranthera*
- 4. Leaves opposite at least below 5. *Arnica*
- 4. Leaves alternate 5
- 5. Phyllaries in a single series, equal; style tips truncate 28. *Senecio*
- 5. Phyllaries in 2 or more series, more or less unequal and graduated 6
- 6. Heads numerous, small, in panicles or cymes, involucre usually 2 to 7 mm high; fibrous rooted plants from a rhizome 29. *Solidago*
- 6. Heads few, and relatively large, involucre more than 7 mm high; plants from a taproot 19. *Haplopappus*

Group D. Rays white to pink, purple, red, or blue.

- 1. Receptacle chaffy or bristly throughout; pappus of graduated bristles, narrow scales, or none ..2
- 1. Receptacle naked; pappus various 3
- 2. Receptacle chaffy throughout; pappus none 1. *Achillea*
- 2. Receptacle densely bristly; pappus of graduated bristles, narrow scales, or reduced 8. *Centaurea*
- 3. Pappus of the disk flowers partly or wholly of capillary bristles 4

- 3. Pappus a short crown, reduced, or none 5
- 4. Rays numerous, filiform, about equal or slightly longer than the disk flowers; annual plants 12. *Conyza*
- 4. Rays larger than the disk flowers ..14. *Erigeron*
- 5. Receptacle conic or hemispheric; leaves pinnately dissected; pappus a minute crown 26. *Matricaria*
- 5. Receptacle flat or nearly so; leaves entire 33. *Townsendia*

Group E. Heads or disciform; pappus capillary

- 1. Receptacle densely bristly or leaves more or less spiny and thistlelike 2
- 1. Receptacle naked; leaves not at all thistlelike, (spiny in species of *Tetradymia*) 3
- 2. Plants thistlelike with spiny-margined leaves; involucre all spiny 11. *Cirsium*
- 2. Plants not thistlelike, leaves not spiny-margined; involucre not spiny (ours with one species lacerate-margined) 8. *Centaurea*
- 3. Shrubs 4
- 3. Herbs 5
- 4. Involucral bracts 4 to 6, equal 32. *Tetradymia*
- 4. Involucral bracts over 6, numerous, imbricate 10. *Chrysothamnus*
- 5. Herbage densely white-woolly; leaves simple, entire, alternate and basal, generally tufted 3. *Antennaria*
- 5. Herbage not at all white-woolly; stems leafy, without basal tuft of leaves 12. *Conyza*

Group F. Heads discoid or disciform; pappus chaffy, or of awns or none

- 1. Involucres, at least in part, covered with hooked prickles, or nutlike or burrlike and armed with tubercles or straight spines 2
- 1. Involucres not as above, all similar 4
- 2. Heads all alike; involucral bracts hooked at the tip; receptacle bristly 4. *Arctium*
- 2. Heads unisexual; involucre of the pistillate heads nutlike or burrlike, armed with hooked prickles, spines or tubercles; staminate involucral heads unarmed; receptacle chaffy 3
- 3. Pistillate involucre with hooked prickles 35. *Xanthium*
- 3. Pistillate involucre with one to several rows of tubercles or spines 16. *Franseria*
- 4. Receptacle chaffy throughout; heads very small, the involucre only 1.5 to 4 mm high 22. *Iva*
- 4. Receptacle naked, or beset with long hairs in *Artemisia* 5
- 5. Involucral bracts herbaceous, not scarious or hya-

- line; pappus of well developed scales 9. *Chaenactis*
5. Involucral bracts definitely scarious or hyaline, at least at the apex; pappus a very short crown, scales, or none 6
6. Involucral bracts nearly equal, pale yellowish, with more or less petaloid tips 21. *Hymenopappus*
6. Involucral bracts not at all petal-like nor yellowish, more imbricate, scarious marginal as well as tips 6. *Artemisia*
1. *Achillea* L. Yarrow
1. *Achillea millefolium* L. Circumboreal, April to October. Webb Springs, Butte Co., 1 July 1967, 1086.
2. *Agoseris* Raf. False Dandelion
1. *Agoseris glauca* (Pursh) Raf. Moist to dry, open places, May to September. British Columbia to Manitoba, south to California, Arizona, and Minnesota. Big Butte, Butte Co., 22 June 1950, AEC 84 (IDS).
3. *Antennaria* Gaertn. Everlasting;
Pussy-toes
1. Perennial stoloniferous plant; heads several or many 2. *A. rosea*
1. Perennial plant, without stolons; heads solitary, terminal 1. *A. dimorpha*
1. *Antennaria dimorpha* (Nutt.) T. & G. Foothills and plains, April to May. British Columbia and Montana, south to California, Nebraska and Colorado. Middle Butte, Bingham Co., 3 May 1956; French 45 (NRTS).
2. *Antennaria rosea* Greene. Dry places on the plains to middle elevations, May to August. Alaska to Ontario, south to California and New Mexico. East Butte, Bingham Co., 22 June 1967, 1019. R.29E., T.7N., Butte Co., 10 June 1967, 934. Birch Creek, Clark Co., 25 June 1967, 1043.
4. *Arctium* L. Burdock
1. *Arctium minus* (Hill) Bernh. A weedy plant of waste places, July to October. Over much of the United States and southern Canada. Birch Creek, Clark Co., 5 September 1967, 1214.
5. *Arnica* L. Arnica
1. *Arnica cordifolia* Hook. Foothills and mountain slopes and woods, April to June. Alaska, south to California and New Mexico; Michigan. Webb Springs, Butte Co., 15 July 1967, 1160.
6. *Artemisia* L. Sagebrush;
Wormwood
1. Plants all shrubs; flowers all perfect 2
1. Plants shrubs or herbs; marginal flowers pistillate 5
2. Heads sessile in the axils and surpassed by the subtending leaves; leaves deciduous, 3 to 5-cleft 5. *A. rigida*
2. Heads not sessile in the axils, upper heads with the subtending leaves not surpassing them; leaves persistent through winter, deeply cleft to merely tridentate 3
3. Flowers mostly 5 to 8 in each head; leaves commonly deeply cleft into narrow segments, these often 3-cleft 8. *A. tripartata*
3. Leaves mostly merely toothed at the apex 4
4. Plants mostly 1 to 4 dm tall; leaves mostly 1.5 to 5 cm long or less 1. *A. arbuscula*
4. Plants taller 4 to 20 dm tall; leaves mostly 1.5 to 5 cm long 7. *A. tridentata*
5. Disk flowers sterile, ovary abortive 6
5. Disk flowers fertile, ovary normal 7
6. Plant spinescent subshrub; achenes and corollas cobwebby with long hairs 6. *A. spinescens*
6. Unarmed herbs; achenes and corolla glabrous 3. *A. dracuncululus*
7. Inodorous (more or less), glabrous, taprooted annual or biennial plant 2. *A. biennis*
7. Aromatic perennial from a rhizome; pubescence white-tomentose 4. *A. ludoviciana*
1. *Artemisia arbuscula* Nutt. var. *nova* (Nels.) Cronq. Dry plains, July to September. Washington to Montana, south to California and New Mexico. South of Junction 88—Lincoln Blvd., Butte Co., 6 September 1967, 1224.
2. *Artemisia biennis* Willd. Along waterways and in sandy soil, August to October. Widely distributed, especially in northwestern United States. Birch Creek, Clark Co., 5 September 1967, 1216.
3. *Artemisia dracuncululus* L. Plains to middle elevations, July to October. Yukon to Manitoba, south to California, Texas, and New Mexico; Eurasia. Big Lost River, Butte Co., 13 July 1967, 1139.
4. *Artemisia ludoviciana* Nutt. var. *latiloba* Nutt. Dry, open places, June to October. British Columbia to Ontario, south to California, New Mexico, and Arkansas. T.3N., R.29E., Butte Co., 11 July 1967, 1129.
5. *Artemisia rigida* (Nutt.) Gray. Mostly on dry, rocky foothills and plains, September to October. Montana to Washington and Oregon. East Butte; Bingham Co., 22 June, 1967, 1013. Big Butte, Butte Co., 26 May 1967, 866.
6. *Artemisia spinescens* Eaton. Plains and foothills, April to June. Montana to Oregon, south to California and New Mexico. T.6N., R.30E., Butte Co., 6 June 1967, 902.
7. *Artemisia tridentata* Nutt. Mostly of lower elevations, but sometimes to timberline, July to September. Widespread in the western United States. Birch Creek, Clark Co., 5 September 1967, 1212.

8. *Artemisia tripartita* Rydb. Dry plains to moist areas in the mountains, July to September. British Columbia to Montana, south to California and Colorado. T.1N., R.30E., Butte Co., August 1965, Harniss, s.n., (UTC).

7. *Balsamorhiza* Nutt. Balsamroot

1. *Balsamorhiza sagittata* (Pursh) Nutt. Valleys and open slopes, April to July. British Columbia to Montana, south to California, South Dakota, and Colorado. Webb Springs, Butte Co., 1 July 1967, 1078.

8. *Centaurea* L. Star-thistle; Knapweed

1. Perennial from creeping roots; involucre greenish-stramineous, middle and outer bracts broad, with subentire hyaline tips 2. *C. repens*

1. Biennial or short-lived perennial from a taproot; involucre greenish, the middle and outer bracts with short, dark pectinate tips

. 1. *C. maculosa*

1. *Centaurea maculosa* Lam. A weedy plant of waste places, June to October. Common in the north-eastern United States, less common westward; Europe. North of Junction 88-22, Butte Co., 5 September 1967, 1221.

2. *Centaurea repens* L. A noxious weed, June to September. Over much of the arid portions of the west, June to September. T.6N., R.31E., Butte Co., 28 July 1967, 1201.

9. *Chaenactis* DC. False yarrow;
Dusty Maiden

1. *Chaenactis douglasii* (Hook.) H. & A. Rocky or sandy soil of the plains and foothills, May to September. British Columbia to Montana, south to California, Colorado and Arizona. R.31E., T.4N., Butte Co., 8 June 1967, 1008.

10. *Chrysothamnus* Nutt.
Rabbit brush

1. Twigs covered by a feltlike tomentum
. 1. *C. nauseosus*

1. Twigs glabrous to minutely puberulent, not tomentose 2. *C. viscidiflorus*

1. *Chrysothamnus nauseosus* (Pall.) Britt. Plains and foothills, August to October. British Columbia to Saskatchewan, south to Texas, New Mexico and California. CFA, Butte Co., 9 September 1955, French, 2, (UTC). South of Junction 88—Lincoln Blvd., 24 August 1967, 1210.

2. *Chrysothamnus viscidiflorus* (Hook.) Nutt. Plains and foothills, July to September. British Columbia to California, east to North Dakota, and New Mexico. South of Junction 88—Lincoln Blvd., Butte Co., 24 August 1967, 1203.

11. *Cirsium* Mill. Thistle

1. *Cirsium vulgare* (Sav.) Airy-Shaw. A weedy plant, July to September. Over much of North America; native of Eurasia. Birch Creek, Clark Co., 5 September 1967, 1213.

12. *Conyza* Less.

1. *Conyza canadensis* (L.) Cronq. A weedy plant, July to September, Southern Canada; Tropical America; over much of the United States. Big Lost River, Butte Co., 13 July 1967, 1146.

13. *Crepis* L. Hawk's-beard

1. Involucres, or lower part of stem, or both conspicuously setose, not glandular 2

1. Involucres and stem slightly or not at all setose, if setose then with gland-tipped setae 3

2. Plants mostly less than 3 dm tall; heads 1 to 9, each with 10 to 60 flowers . . . 3. *C. modocensis*

2. Plants usually 3 to 8 dm tall; heads 6 to 70, each with 8 to 25 flowers 2. *C. barbiger*

3. Well developed plants 2 to 7 dm tall, with 20 to 100 heads; herbage gray-tomentose to glabrate above; heads 5 to 10 flowered . . 1. *C. acuminata*

3. Plants smaller 0.5 to 4 dm tall, with 2 to 25 heads; often glandular-hirsute above; heads 10 to 40 flowered 4. *C. occidentalis*

1. *Crepis acuminata* Nutt. Foothills to moderate elevations, May to July. Montana to Washington, south to California and New Mexico. Sec. 29, T.3N., R.28E., Butte Co., 18 June 1956, McBride, s.n., (NRTS).

2. *Crepis barbiger* Leib. ex Coville. Dry plains and foothills, May to July. Oregon to Washington, east to central and northern Idaho. R.29E., T.7N., Butte Co., 9 June 1967, 921.

3. *Crepis modocensis* Greene ssp. *modocensis*. Plains and foothills, May to July. British Columbia to Montana, south to Wyoming, and Colorado, and California. Big Butte, Butte Co., 20 June 1950, AEC, (IDS).

4. *Crepis occidentalis* Nutt. ssp. *occidentalis*. Plains and foothills, May to July. British Columbia to California, east to South Dakota, and New Mexico. R.31E., T.6N., Butte Co., 8 June 1967, 909.

14. *Erigeron* L. Daisy;
Fleabane

1. Leaves trifid to ternately dissected; rays reduced or wanting 1. *E. compositus*

1. Leaves entire to toothed; rays well developed . . 2

2. Rays well over 100; plants fibrous rooted 3. *E. glabellus*

2. Rays 100 or less; plants from a taproot 3

3. Lower leaves with 3 more or less prominent veins; rays 35 to 65 2. *E. corymbosus*

3. Leaves not trinerved; rays 50 to 100

1. *Erigeron compositus* Pursh. Dry sand or rocky ground, May to August. Greenland to California, Arizona, South Dakota, and Quebec. T.4N., R.28E., Butte Co., 21 May 1967, 804A.

2. *Erigeron corymbosus* Nutt. Sagebrush plains and slopes, June to July. British Columbia to Montana, south to Oregon and Wyoming. Big Butte, Butte Co., 15 July 1967, 1156.

3. *Erigeron glabellus* Nutt. Along rivers and other moist places, June to July. Alaska to Utah, South Dakota, and Wisconsin. Big Lost River, Butte Co., 13 July 1967, 1152.

4. *Erigeron pumilus* Nutt. Plains and foothills, May to July. British Columbia to Saskatchewan, south to California and New Mexico. Big Lost River, Butte Co., 13 July 1967, 1148. Middle Butte, Bingham Co., 22 June 1967, 1031.

15. *Eriophyllum* Lag.

1. *Eriophyllum lanatum* (Pursh) Forbes var. *integrifolium* (Hook.) Smiley. Dry plains to moderate elevations in the mountains, May to August. Widespread east of the Cascades. South slope of East Butte, Bingham Co., 22 June 1967, 1007A.

16. *Franseria* Cav.

1. *Franseria acanthicarpa* (Hook.) Cov. Mostly along streams in sandy soil, July to October. Saskatchewan to Washington, south to California and Texas. R.31E., T.6N., Butte Co., 18 July 1967, 1165A. Payne (1964) has placed *Franseria* as synonymy under *Ambrosia*.

17. *Grindelia* Willd. Gum Plant; Resinweed

1. *Grindelia squarrosa* (Pursh) Dunal. var. *serrulata* (Rydb.) Steyerl. Dry, open places, July to September. British Columbia to Minnesota, south to California and Texas. T.3N., R.28E., Butte Co., 28 July 1967, 1181.

18. *Gutierrezia* Lag. Matchbrush; Snakeweed

1. *Gutierrezia sarothrae* (Pursh) Britt. & Rusby. Plains and foothills, July to September. Saskatchewan, south to California, Mexico, and Kansas. Tractor Flat, Jefferson Co., 22 July 1967, 1203A.

19. *Halopappus* Cass.

1. Low branching shrubs, not caespitose

1. Caespitose plant, with herbaceous flowering stems

1. *Haplopappus acaulis* (Nutt.) Gray Foothills to well up in the mountains, May to August. Saskatch-

ewan to Colorado, west to Montana, central Idaho, Oregon and California. R.38E., T.4N., Butte Co., 21 May 1967, 805.

2. *Haplopappus nanus* (Nutt.) Eaton Gravelly soil and rocky ledges, May to August. Idaho, west to Washington and California, south to Utah. Big Butte, Butte Co., 28 May 1938, Davis, 161, (IDS).

20. *Helianthus* L. Sunflower

1. *Helianthus petiolaris* Nutt. Plains, usually in waste places. June to September. Widespread in the United States. R.31E., T.6N., Butte Co., 2 July 1967, 1111.

21. *Hymenopappus* L'Her

1. *Hymenopappus filifolius* Hook. Gravelly or sandy soil of the plains, May to July. Washington to California, east to North Dakota and Texas. R.30E., T.6N., Butte Co., 11 June 1967, 944.

22. *Iva* L.

1. Annual; leaves long-petiolate . . . 1. *I. xanthifolia*

1. Perennial from a creeping rootstock; leaves sessile or subpetiolate 1. *I. axillaris*

1. *Iva axillaris* Pursh. Plains and foothills, often in alkaline soil, May to September. Manitoba to British Columbia, south to California and Oklahoma. Big Lost River, Butte Co., 13 July 1967, 1137.

2. *Iva xanthifolia* Nutt. Along streams and in bottomlands, August to October. Alberta to Washington, south to New Mexico and Texas. Sec. 17, T.3N., R.30E., Butte Co., 2 August 1956, McBride, 79, (NRTS).

23. *Lactuca* L. Lettuce

1. Biennial or winter annual; leaves prickly on the midrib beneath and on the margins; heads relatively small 2. *L. scariola*

1. Perennial; leaves glabrous or glabrate, not prickly heads large and showy 1. *L. pulchella*

1. *Lactuca pulchella* (Pursh) DC. Moist places, June to September. Alaska to California, east to Minnesota and Missouri. T.2N., R.30E., Bingham Co., 23 July 1967, 1173.

2. *Lactuca scariola* L. A weedy plant of fields and waste places, July to September. Europe; over much of the United States. North of Highway 20, east side, Bingham Co., 29 September 1955, French, 9, (NRTS).

24. *Lygodesmia* D. Don Rush Pink; Skeleton-weed

1. Branches spine-tipped, divaricate, rigid; involucre imbricate, 7 to 13 mm long 2. *L. spinosa*

1. Branches not spine-tipped; involucre merely calyculate, 18 to 22 mm long . . . 1. *L. grandiflora*

1. *Lygodesmia grandiflora* (Nutt.) T. & G. Foothills and valleys May to July. Idaho and Wyoming to

California and New Mexico. T.3N., R.38E., Butte Co., 11 July 1967, 1128.

2. *Lygodesmia spinosa* Nutt. Dry, rocky or sandy places, July to August. British Columbia to Montana, south to California and Arizona. Tractor Flat, Jefferson Co., 22 July 1967, 1200.

25. *Machaeranthera* Eaton

1. *Machaeranthera canescens* Gray. Dry, open places of the plains and foothills, July to October. Saskatchewan to British Columbia, south to California and Colorado. Big Butte, Butte Co., 7 September 1967, 1232.

26. *Matricaria* L.

1. *Matricaria maritima* L. A weed of waste places and roadsides, July to September. Europe; widely established in North America. R. 29E., T.3N., Butte Co., 11 July 1967, 1132.

27. *Microseris* D. Don

1. *Microseris troximoides* Gray. Dry, open places in the foothills and plains, April to June. British Columbia, south to California, Montana and northern Utah. R.29E., T.7N., Butte Co., 10 June 1967, 929.

28. *Senecio* L. Groundsel; Butterweed

1. Cauline leaves well developed, with well developed tuft of basal leaves; glabrous or puberulent near the base 3. *S. serra*

1. Basal leaves well developed and the cauline leaves gradually reduced upwards; crisp-villous to arachnoid-villous or densely tomentose 2

2. Pubescence loosely crisp-villous or arachnoid-villous, sometimes sparse at flowering time; stems solitary 2. *S. integerrimus*

2. Pubescence strongly white-tomentose; stems usually several 1. *S. canus*

1. *Senecio canus* Hook. Plains and foothills, May to August. Saskatchewan to British Columbia, south to California, Colorado, and Nebraska. R.29E., T.3N., Butte Co., 1 July 1967, 1092.

2. *Senecio integerrimus* Nutt. Plains to high in the mountains, May to July. British Columbia to California, east to Saskatchewan and Minnesota. R.31E., T.6N., Butte Co., 11 June 1967, 942.

3. *Senecio serra* Hook. Open places in the foothills to middle elevations in the mountains, south to California and Colorado. Webb Springs, Butte Co., 15 July 1967, 1158.

29. *Solidago* L. Goldenrod

1. *Solidago occidentalis* (Nutt.) T. & G. Stream-banks and other moist areas, July to October. Alberta to British Columbia, south to California, New Mexico, and Nebraska. Big Lost River, Butte Co., 13 July 1967, 1149.

30. *Stephanomeria* Nutt. Rush Pink; Skeletonweed

1. Annual or biennial; pappus bristles plumose on the upper 1/2 to 2/3; achenes rugose-tuberculate and pitted 1. *S. exigua*

1. Perennial; pappus bristles plumose to the base; achenes smooth 2. *S. tenuifolia*

1. *Stephanomeria exigua* Nutt. Plains and foothills in dry, often sandy soil. June to August. Central Oregon to Wyoming, south to California and New Mexico. T.3N., R.29E., Butte Co., 18 July 1967, 1169.

2. *Stephanomeria tenuifolia* (Torr.) Hall. Plains and foothills to middle elevations, June to September. British Columbia and Washington to Montana, south to California and Texas. Junction of Highway 22-Atomic City, Butte Co., 14 July 1967, 1153.

31. *Taraxacum* Hall Dandelion

1. *Taraxacum officinale* Webber in Wiggers. A weedy plant, March to December. Cosmopolitan; native of Europe and adjacent Asia. Sec. 10, T.2N., R.29E., Butte Co., 3 August 1956, McBride, 36, (NRTS).

32. *Tetradymia* DC. Horse Brush

1. Primary leaves forming spines; flowers 5 to 9 ... 2. *T. spinosa*

1. Primary leaves not forming spines; flowers 4 ... 1. *T. canescens*

1. *Tetradymia canescens* DC. Foothills and plains, June to September. British Columbia to Montana, south to California and New Mexico. R.31E., T.4N., Butte Co., 18 July 1967, 1171.

2. *Tetradymia spinosa* H. & A. Foothills and plains, May to August. Southwestern Montana and central Idaho to Oregon, south to Colorado, and Utah. T.6N., R.30E., Butte Co., 6 June 1967, 903. R. 34E., T.5N., Jefferson Co., 20 June 1967, 1004.

33. *Townsendia* Hook. Daisy

1. *Townsendia florifer* (Hook.) Gray. Plains and foothills, May to July. Washington to Idaho, south to Nevada, Utah and Wyoming. T.4N., R.28E., 21 May 1967, 804.

34. *Tragopogon* L. Goatsbeard

1. *Tragopogon dubius* Scop. Dry ground, especially along roadsides, May to July. Over much of the United States; Europe. T.6N., R.31E., Butte Co., 29 July 1967, 1184. R.34E., T.5N., Jefferson Co., 20 June 1967, 988.

35. *Xanthium* L. Cocklebur

1. *Xanthium strumarium* L. var. *canadense* (Mill.) T. & G. Disturbed ground, April to October. Cosmopolitan. Sec. 33, T.5N., R.30E., Butte Co., 26 July 1956; French, 75, (NRTS).

CONVOLVULACEAE. MORNING-GLORY
FAMILY1. *Convolvulus* L. Bindweed;
Morning-glory

1. *Convolvulus arvensis* L. A very troublesome weed introduced from Europe and now well established in North America. May to August. T.2N., R.30E., Butte Co., 3 July 1967, 1116.

CORNACEAE. DOGWOOD FAMILY

1. *Cornus* L. Dogwood

1. *Cornus stolonifera* Michx. Common along streams and in moist woods, May to July. Widespread in North America. Webb Springs, Butte Co., 1 July 1967, 1087. Birch Creek, Clark Co., 25 June 1967, 1052.

CRASSULACEAE. STONECROP

1. *Sedum* L. Stonecrop

1. *Sedum stenopetalum* Pursh. Variable in habitat from the sagebrush plains to subalpine ridges, May to July. Western temperate North America. Big Butte, Butte Co., 1 July 1967, 1106.

CRUCIFERAE. MUSTARD FAMILY

1. Pods stipitate; stipe 1 mm long or more 2
1. Pods not stipitate or stipe less than 1 mm long 3
2. Stipe 5 mm long or less; petals white or purple 15. *Thelypodium*
2. Stipe over 5 mm long, mostly 1 to 3 cm long; petals yellow 14. *Stanleya*
3. Silique composed of two distinct segments, upper segment commonly sterile; beak stout, over 5 mm long 2. *Brassica*
3. Pods composed of one segment, seed bearing; beak not stout 4
4. Fruit a silique 5
4. Fruit a silicle 17
5. Petals yellow 6
5. Petals never yellow, white to purple 10
6. Plants with appressed, mostly 2-forked hairs; stigmas deeply 2-lobed 5. *Erysimum*
6. Plants glabrous or if pubescent not as above 7
7. Petals about 2 mm long; seeds biseriate, sometimes uniseriate in *Descurainia* 8
7. Petals over 2 mm long; seeds uniseriate 9
8. Plants aquatic or semiaquatic; fruit 1-nerved; pubescence not stellate 11. *Rorippa*
8. Plants terrestrial; fruit several-nerved; pubescence stellate 4. *Descurainia*
9. Valves of the silique with a prominent midnerve; plants not rhizomatous; annual or biennial 13. *Sisymbrium*
9. Valves indistinctly nerved; plants rhizomatous perennials 12. *Schoenocrambe*
10. Perennial, caespitose plants from a branched cau-

dex; leaves entire, mostly basal; pubescence grayish with branched hairs; petals 10 to 15 mm long

- 10. *Phoenicautis*
10. Plants erect, not as above; leaves toothed to lobed or smaller with the petals less than 10 mm long 11
11. Seeds biseriate; pods terete 6. *Halimilobos*
11. Seeds uniseriate 12
12. Pubescence not branched or lacking 13
12. Pubescence branched to stellate 14
13. Stamens tetradynamous; pods strongly flattened parallel to the partition; style lacking 1. *Arabis*
13. Stamens 6; pods terete or 4-sided, not flattened; style short 15. *Thelypodium*
14. Leaves 1 to 3 times pinnately compound 4. *Descurainia*
14. Leaves mostly simple, at least the cauline so 15
15. Pods strongly flattened parallel to the partition; leaves simple 1. *Arabis*
15. Pods terete or 4-sided (or nearly so); leaves simple to bipinnatifid 16
16. Annuals; flowers bracteate 9. *Malcolmia*
16. Biennial or perennials; flowers ebracteate 6. *Halimilobos*
17. Silicles strongly flattened, not turgid 18
17. Silicles not strongly flattened, if so weakly, distinctly turgid 19
18. Fruit 1-loculed and 1-seeded; silicle broadly winged 17. *Thysanocarpus*
18. Fruit 2-loculed, several seeded; silicle only slightly winged 8. *Lesquerella*
19. Pods inflated, nearly globose to oblong-rotund 8. *Lesquerella*
19. Pods more or less obcompressed 20
20. Seeds 1 per locule; pubescence simple, when present 7. *Lepidium*
20. Seeds 2 to many per locule; pubescence stellate, when present 21
21. Fruit triangular in shape; plants hirsute and stellate; silicles not wing-margined 3. *Capsella*
21. Fruit not triangular; plants glabrous; silicles wing-margined all around 16. *Thlaspi*

1. *Arabis* L. Rock Cress

1. Siliques erect, not over 2 mm broad; seeds with a wing 0.3 mm broad or less, wingless; stems simple 5. *A. nuttallii*
1. Siliques erect to reflexed; seeds winged, the wing 0.3 mm broad or more 2
2. Plants usually less than 2 dm tall; silique various but not reflexed; stems 1 mm thick or less 4. *A. microphylla*
2. Plants mostly over 3 dm tall; siliques frequently reflexed 3
3. Leaves mostly densely pubescent, never ciliate; siliques spreading to pendulous, not sharply reflexed; cauline leaves auriculate 4

3. Leaves not densely pubescent, greenish to grayish, ciliate or the siliques sharply reflexed, or the stem leaves not auriculate 5
4. Petals 4 to 6 mm long; seeds with a wing at least 0.5 mm broad; style short 1. *A. cobrensis*
4. Petals 6 to 9 mm long; wing of the seeds less than 0.5 mm broad; style lacking 3. *A. lignifera*
5. Lower cauline leaves usually petiolate; siliques 3 to 7 cm long; 1-nerved to about midlength 2. *A. holboellii*
5. Lower cauline leaves usually auriculate; siliques 4 to 12 cm long, 1-nerved for nearly the full length 6. *A. sparsiflora*

1. *Arabis cobrensis* Jones. Sagebrush hills and plains, May to July, Wyoming, east across south central Idaho, to central Oregon and northern Nevada. Near Big Butte, Butte Co., s.n., Davis, 167, (IDS). R.29E., T.3N., Butte Co., 6 June 1967, 882.

2. *Arabis holboellii* Hornem. var. *retrofacta* (Grah.) Rydb. Sagebrush plains to higher elevations in the mountains, May to August. Montana, north to British Columbia, south to California, east to Colorado. R.28E., T.4N., 20 May 1967, 797.

3. *Arabis lignifera* A. Nels. In sagebrush areas, May to June. Wyoming, Idaho to Arizona and Nevada. N.W. sec. 4, T.3N., R.28E., Butte Co., 18 May 1954, Fineman, 152, (UTC).

4. *Arabis microphylla* Nutt. in T. & G. var. *saximontana* Rollins. Commonly in the lower montane areas and higher mountains, April to July. Montana and Wyoming, to Idaho, and Utah. Webb Springs, Butte Co., 22 May 1967, 829. East Butte, Bingham Co., 18 May 1967, 774.

5. *Arabis nuttallii* Robin. Low valleys to higher in the mountains, April to August. Alberta to eastern Washington and Nevada, south to Wyoming, Idaho and Utah. R.29E., T.7N., Butte Co., 10 June 1967, 928.

6. *Arabis sparsiflora* Nutt. var. *sparsiflora*. Sagebrush plains, April to June. Idaho, Utah to north-eastern California. Dry plains on Little Lost River, Butte Co., 30 May 1938, probably Davis, 162, (IDS). This plant should be looked for on the NRTS, particularly on the N.W. portion of the site.

2. Brassica L. Mustard

1. *Brassica juncea* (L.) Coss. Commonly a weed along roadsides and in waste places, May to August. Common throughout North America; Native of Europe, T.2N., R.30E., Bingham Co., 23 July 1967, 1174.

3. Capsella Medic. Shepherds purse

1. *Capsella bursa-pastoris* (L.) Medic. A weed, March to July. Common throughout most of North America. Atomic City, Bingham Co., 1 July 1967, 1089.

4. Descurainia Webb. & Berth.

Tansy mustard

1. Pods subclavate to clavate 2. *D. pinnata*
1. Pods linear, not enlarged at the apex 2
2. Leaves 2 to 3 times pinnate; pods over 20-seeded 4. *D. sophia*
2. Leaves only pinnate; pods less than 20-seeded ...3
3. Siliques fusiform; style commonly over 0.5 mm long 1. *D. californica*
3. Siliques not fusiform; style less than 0.5 mm long 3. *D. richardsonii*

1. *Descurainia californica* (Gray) Schulz. Wyoming to Oregon, south through the Great Basin. Big Butte, Butte Co., 27 June 1950, AEC, 119, (IDS).

2. *Descurainia pinnata* (Walt.) Britt. var. *filipes* (Gray) Peck. A weedy and common species, April to July. Throughout most of southern Canada and the United States. Big Butte, Butte Co., 26 June 1950, AEC, 111, (IDS).

3. *Descurainia richardsonii* (Sweet) Schulz. Plains to Middle elevations, June to August. Throughout western North America. Big Butte, Butte Co., 22 June 1950, AEC, 82, (IDS).

4. *Descurainia sophia* (L.) Webb. A weedy plant along roadsides and in cultivated areas, March to July. Europe; Most of North America. T.4N., R.31E., Butte Co., 20 May 1967, 783.

5. Erysimum L. Wallflower

1. Pedicels 4 to 8 mm long; petals pale yellow, 7 to 11 mm long 2. *E. inconspicuum*
1. Pedicels 8 to 13 mm long; petals yellow to deep orange or somewhat reddish, 15 to 25 mm long 1. *E. asperum*
1. *Erysimum asperum* (Nutt.) DC. In our area commonly in sagebrush, May to July. In most of the western states, to Minnesota, Kansas, and Oklahoma. Arco, Butte Co., 17 May 1936, Girst, s.n., (IDS). Near Big Butte, Butte Co., 29 May 1938, Davis, 164, (IDS).

2. *Erysimum inconspicuum* (Wats.) MacMillan. Plains, often in alkaline soil, June to July. Ontario to Alaska, south to southeastern Oregon, and Montana, to Colorado; central United States. Near Big Butte, Butte Co., 29 May 1938, Davis, 164, (IDS).

6. Halimolobos Tausch.

1. Seeds biseriate; siliques glabrous; cauline leaves auriculate 2. *H. virgata*
1. Seeds uniseriate; siliques hairy; cauline leaves sessile but not auriculated 2
2. Siliques not constricted between the seeds, consistently stellate; leaves mostly entire; stigma not lobed, rounded 3. *H. whitedii*
2. Siliques strongly torulose, sometimes glabrate; leaves commonly lyrate; stigma often lobed 1. *H. perplexa*

1. *Halimolobos perplexa* (Henderson) Rollins. Dry soil and loose rocky areas, May to June. Central and west-central Idaho. Big Butte, Butte Co., 20 June 1950, AEC, (IDS).

2. *Halimolobos virgata* (Nutt.) Schulz. Open plains and foothills, June to July. Yukon to Saskatchewan, to central Idaho to Wyoming, Utah and Colorado. Big Creek, Butte Co., 30 May 1938, Davis, 178, (IDS). Should be looked for on the site.

3. *Halimolobos whitedii* (Piper) Rollins. Sagebrush and desert plains, May to June. Central Washington and Bingham County, Idaho. East Butte, Bingham Co., 22 June 1967, 1024.

7. *Lepidium* L. Pepper grass

1. Style present; cauline leaves auriculate to perfoliate 2. *L. perfoliatum*

1. Style lacking; cauline leaves not auriculate or perfoliate 2

2. Petals usually lacking or rudimentary; pods oblong to obovate 1. *L. densiflorum*

2. Petals sometimes present; pods elliptic to oval 3. *L. virginicum*

1. *Lepidium densiflorum* Schrad. var. *macrocarpum* Mulligan. Dry soil, April to June. Eurasia; now widespread in North America. This variety occurs from Alaska to California, and Arizona, east to Montana and Colorado. R.30E., T.6N., Butte Co., 11 June 1967, 948.

2. *Lepidium perfoliatum* L. Dry, waste ground, March to June. Native of Europe and now well established in the western and central part of the United States. Sec. 12, T.6N., R.33E., Jefferson Co., 6 June 1956, McBride, 56, (NRTS).

3. *Lepidium virginicum* L. var. *medium* (Greene) C. L. Hitchc. Becoming a weedy plant, March to June. Northern California to eastern Washington, east through Idaho to Wyoming, south to Arizona, New Mexico, and Texas. Butte Co., June 1950, AEC, 142, (IDS).

8. *Lesquerella* Wats. Bladder-pod

1. Pedicles uniformly recurved, not straight or sigmoid; fruit globose; leaves mostly narrowly oblanceolate 2. *L. ludoviciana*

1. Pedicels sigmoid or straight; fruit ovate to oblong; leaves broader than oblanceolate 1. *L. alpina*

1. *Lesquerella alpina* (Nutt.) Wats. var. *laevis* (Pays.) C. L. Hitchc. Dry plains and foothills and mountain ridges, May to July. Alberta, south to Montana, and western South and North Dakota, west to Colorado and central and southeastern Idaho. R.30E., T.6N., Butte Co., 11 June 1967, 945. Should be looked for on the site.

2. *Lesquerella ludoviciana* (Nutt.) Wats. Probably var. *ludoviciana*. Mostly of the plains, May to June.

Eastern Montana to the Dakotas, Minnesota and Illinois, south to central Idaho, Utah, and Colorado. Six miles S.W. of Atomic City, Butte Co., 26 May 1967, 861.

9. *Malcolmia* (L.) R. Br.

1. *Malcolmia africana* (Willd.) R. Br. Becoming a weedy plant in Colorado, south and central Idaho, Nevada and Arizona; native of Africa, April to June. T.2N., R.31E., Bingham Co., 22 June 1967, 1026. Junction of Highway 28-22, Clark Co., 25 May 1967, 852.

10. *Phoenicaulis* Nutt.

1. *Phoenicaulis cheriranthoides* Nutt. in T. & G. Sagebrush plains and hills, April to June. Idaho to central Washington, south to Nevada and California. North slope of Big Butte, 26 May 1967, 878.

11. *Rorippa* Scop. Yellow water-cress

1. *Rorippa nasturtium-aquaticum* (L.) Schinz. & Thell. Along streams and other fresh water bodies, in shallow water. March to October. Native of Europe, now well established in North America. Birch Creek, Clark Co., 25 June 1967, 1021.

12. *Schoenocrambe* Greene

1. *Schoenocrambe linifolia* (Nutt.) Greene. Mostly in sagebrush and juniper plains, May to June. British Columbia, south to Nevada, east to Montana, south to Idaho and Utah. Arco Desert, Butte Co., 16 May 1936, Davis, s.n., (IDS). R.29E., T.4N., Butte Co., 22 May 1967, 819.

13. *Sisymbrium*

1. *Sisymbrium altissimum* L. Mostly along roadsides and in waste places, weedy, May to September. Native to Europe, well established in the United States. R.30E., T.6N., Butte Co., 12 June 1967, 959.

14. *Stanleya* Nutt. Prince's plume

1. *Stanleya viridiflora* Nutt. Dry plains and valleys, June to August. Wyoming, west through central Idaho to central Oregon and Montana, south to Utah and Nevada. T.4N., R.31E., Butte Co., 4 July 1967, 1117.

15. *Thelypodium* Endl.

1. Cauline leaves sagittate or clasping at base; stipe less than 2 mm long 2. *T. sagittatum*

1. Cauline leaves not as above; stipe 2 to 4 mm long 1. *T. laciniatum*

1. *Thelypodium laciniatum* (Hook.) Lindl. var. *milleflorum* (Nels.) Pays. Deserts and plains, April to July. Wide spread in western North America. Near Big Butte, Butte Co., 29 May 1938, (IDS).

2. *Thelypodium sagittatum* (Nutt.) Endl. Common in valleys, deserts, and lower mountain areas, usually somewhat moist ground. June to July. Mon-

tana to Idaho and Wyoming, west to Washington, Oregon and California. Birch Creek, Clark Co., 25 June 1967, 1045. Arco, Butte Co., 16 May 1956, no author, s.n., (IDS).

16. *Thlaspi* L. Penny cress

1. *Thlaspi arvense* L. A common weed in North America, April to August. Webb Springs, Butte Co., 26 May 1967, 871. Birch Creek, Clark Co., 25 June 1967, 1048.

17. *Thysanocarpus* Hook. Fringe Pod

1. *Thysanocarpus curvipes* Hook. Moist, often open hillsides; April to June. British Columbia to California, east to Idaho. Arco Desert, Butte Co., 20 May 1956, Quinn, s.n., (IDS).

EUPHORBIACEAE. SPURGE FAMILY

1. *Euphorbia* L. Spurge

- 1. Plants prostrate; stipules present; seeds with transverse ridges 2. *E. glyptosperma*
- 1. Plants erect; stipules lacking; seeds smooth 1. *E. esula*
- 1. *Euphorbia esula* L. Mostly weedy, May to July. Eurasia; over much of the United States. Big Lost River, Butte Co., 11 July 1967, 1130.
- 2. *Euphorbia glyptosperma* Englm. Dry, sandy soil of the plains. June to September. Idaho, west from British Columbia to California, east to New York, south to Texas. T.6N., R.31E., Butte Co., 29 July 1967, 1186.

FUMARIACEAE. FUMITORY FAMILY

1. *Corydalis* Medic.

1. *Corydalis aurea* Willd. In moist and dry habitats, variable, May to July. Nova Scotia, west to Alaska, south to Pennsylvania, New Mexico and California. Arco Desert, Butte Co., June 1950, AEC Project, 6, (IDS), (IDS).

GERANIACEAE. GERANIUM FAMILY

1. *Erodium* L. 'Her. Stark's-bill

1. *Erodium cicutarium* (L.) L.'Her. Native of Eurasia and Africa, April to July. Widespread in the United States. Lost River, Butte Co., 11 July 1930, Davis, s.n., (IDS).

GROSSULARIACEAE. CURRENT AND GOOSEBERRY FAMILY

1. *Ribes* L. Currents and Gooseberries

- 1. Flowers glabrous, bright yellow . . . 1. *R. aureum*
- 1. Flowers pubescent glandular, or both, not bright yellow 2
- 2. Hypanthium twice as long as the sepals; berries 5 to 7 mm in diameter, red 2. *R. cereum*
- 2. Hypanthium about equal to the sepals; berries 10 to 12 mm in diameter, blue to black 3. *R. viscosissimum*

1. *Ribes aureum* Pursh. In moist wooded areas in the mountains to stream banks at lower elevations, April to May. Idaho, west to north central Washington to California, east to the Rocky Mountains from Saskatchewan and South Dakota to New Mexico. Webb Springs, Butte Co., 22 May 1967, 824. Big Lost River, Butte Co., 13 July 1967, 1136.

2. *Ribes cereum* Dougl. var. *inebrians* (Lindl.) Hitchc. Variable in habitat from dry rocky areas to moist shaded areas, April to June. Central Idaho to central Montana, east to Nebraska, south to Utah and Nevada. Webb Springs, Butte Co., 26 May 1967, 875.

3. *Ribes viscosissimum* Pursh. Along creeks, open areas, from moist areas to dry plains, May to June. Idaho, west to the Cascade Mountains, from British Columbia to northwestern Colorado. T.6N., R.30E., Butte Co., 18 May 1967, 760.

HYDROPHYLLACEAE. WATERLEAF FAMILY

- 1. Flowers mostly solitary; leaves entire 3
- 1. Flowers in scorpioid or subcapitate cymes; leaves entire to pinnately lobed or dissected 2
- 2. Flowers in scorpioid cymes; placenta narrow 4. *Phacelia*
- 2. Flowers in subcapitate clusters; placenta broad 2. *Hydrophyllum*
- 3. Plants acaulescent, perennial mesophytes 1. *Hesperochiron*
- 3. Plants caulescent; annual xerophytes . . . 3. *Nama*

1. *Hesperochiron* Wats.

1. *Hesperochiron punilus* (Griseb.) Porter. In the lower foothills and valleys to meadow lands in the mountains, April to June. Idaho, west from Washington to California, east and south from Montana to Colorado, Utah, and Arizona. Five miles south of Atomic City, Butte Co., 22 May 1967, 820.

2. *Hydrophyllum* L. Waterleaf

1. *Hydrophyllum occidentale* Gray. Mostly in moist places in the woods, April to July. Elmore and Jefferson County, Idaho, east to Oregon and California, south to Utah and Arizona. R.34E., T.5N., Jefferson Co., 20 June 1967, 1001.

3. *Nama* L.

1. *Nama densum* Lemmon var. *parviflorum* (Greene) Hitchc. Sandy soil of the plains, May to July. Washington to California, east to Idaho, Nevada, Utah, and Wyoming. Sec., 24, T.3N., R.30E., Butte Co., 25 June 1957, 134, Goodwin, (NRTS).

4. *Phacelia* Juss

- 1. Leaves mostly entire 2
- 1. Leaves pinnatifid or pinnately compound 3
- 2. Plants perennial; stamens strongly exerted 3. *P. hastata*

2. Plants annual; stamens barely exerted or included 4. *P. humilis*
3. Filaments long exerted; ovules and seeds 4 or less; style cleft to near the base 2. *P. glandulosa*
3. Filaments included; ovules and seeds more than 4, style cleft $\frac{1}{4}$ of its length ... 1. *P. glandulifera*
1. *Phacelia glandulifera* Piper. Commonly in sagebrush or sandy soil of the plains, May to June. Washington to California, east through central Idaho to Wyoming and to Nevada. Shell Road, Butte Co., 23 May 1967, 837.

2. *Phacelia glandulosa* Nutt. Rocky ridges of the plains and mountains, June to August. Central Idaho to Montana, Colorado and Utah. Plot 4, Snake River Plains, Butte Co., 17 July 1950, AEC, 82, (IDS).

3. *Phacelia hastata* Dougl. ex Lehm. In a wide variety of habitats, May to August. British Columbia, east to Colorado and Nebraska. East Butte, Bingham Co., 22 June 1967, 1018. Shell Road, Butte Co., 8 June 1967, 923b.

4. *Phacelia humilis* T. & G. Mostly in fairly moist habitats, May to July. Washington to California, east to Nevada, Utah, and Idaho. Webb Springs, Butte Co., 13 June 1967, 969.

LABIATAE. MINT FAMILY

1. Agastache Clayton

1. *Agastache urticifolia* (Benth.) Kuntze. Foothills and mountain slopes, June to August. British Columbia, south to Colorado. Webb Springs, Butte Co., 1 July 1967, 1081.

LEGUMINOSAE. PEA FAMILY

1. Fertile stamens 5, flowers small in dense spikes, corolla irregular 8. *Petalostemon*
1. Fertile stamens usually 10; flowers papilionaceous 2
2. Stamens separate; corolla yellow, racemose 10. *Thermopsis*
2. Flowers not yellow, or if so then the stamens united (stamens mostly united) 3
3. Leaves glandular-punctate and 3-foliolate or the fruit with hooked spines 4
3. Leaves not glandular-punctate or if so then the leaves not 3-foliolate or with hooked spines on the fruit 5
4. Plants 1.5 to 5 dm tall; leaves mostly 3-foliolate, fruit not spiny 9. *Psoralea*
4. Plants usually larger, 3 to 12 dm tall; leaflets 7 to 15; fruit spiny 2. *Glycyrrhiza*
5. Leaves even-pinnate, terminal portion modified into tendrils 11. *Vicia*
5. Leaves with a terminal leaflet, odd-pinnate or trifoliolate 6
6. Leaves palmately compound or trifoliolate; flowers in elongate racemes or heads 9

6. Leaves not palmately compound 7
7. Fruit a loment; keel longer than the wings 3. *Hedysarum*
7. Fruit not a loment; keel shorter than the wings 8
8. Plant mostly without leafy stems; keel beaked 7. *Oxytropis*
8. Plant usually with leafy stems; keel not beaked 1. *Astragalus*
9. Leaves palmately compound 4. *Lupinus*
9. Leaves trifoliolate 10
10. Pods falcate to coiled, heavily veined 5. *Medicago*
10. Pod straight or nearly so, lightly veined 6. *Melilotus*
1. *Astragalus* L. Locoweed; Milk vetch
1. Flowers ascending to erect, in a subcapitate raceme, purplish; legumes erect, villous 1. *A. agrestis*
1. Flowers spreading to descending or less commonly erect; the raceme subcapitate to elongate, ochroleucous to bluish or purplish; legumes various but if erect not villous 2
2. Leaflets 3 to 7, the petioles persistent as a thatch at the base of plant; legumes commonly curved, bilocular and sessile 2. *A. calycosus*
2. Leaflets various in number, commonly more than 7; petioles usually not persistent; legumes various, but if bilocular than bladdery inflated or woody to leathery and straight 3
3. Plants acaulescent; leaves and peduncles arising from the apex of the caudex branches; legumes woolly-villous; calyx tubular-cylindric 10. *A. purshii*
3. Plants with well developed stems; leaves and peduncles arising from well separated nodes; legumes strigose-glabrate or glabrous 4
4. Plants from elongate, subrhizomatous branches; terminal leaflet confluent with the rachis; legumes 1-loculed, bladdery inflated, purplish mottled 4. *A. ceramicus*
4. Plants from caudices, the caudex branches not or seldom (except in *A. miser*) subrhizomatous; terminal leaflet jointed to the rachis; legumes various, but if bladdery inflated then 2-loculed 5
5. Calyx tube cylindric, over 5 mm long 6
5. Calyx tube campanulate, less than 5 mm long 9
6. Ovaries and legumes stipitate, the stipe more than 2.5 mm long, the body of the legume curved or straight at maturity 7
6. Ovaries and legumes sessile, the body of the legume straight to slightly curved at maturity 8
7. Body of the legume curved at maturity; calyx gibbous-saccate dorsally behind the pedicel 6. *A. curvicaupus*
7. Body of the pod nearly or quite straight; calyx not gibbous-saccate 7. *A. filipes*

8. Flowers bluish to purplish, the wing tips whitish; legumes unilocular; plants flowering in early spring 5. *A. cibarius*
8. Flowers ochroleucous, the keel tip purplish; legumes bilocular; plants flowering in late spring or early summer 3. *A. canadensis*
9. Flowers with distinctly purplish veins; keel tip produced into an elongate point at right angles to the keel; legumes unilocular, spreading to descending; leaflets more than three times longer than broad 9. *A. miser*
9. Flowers lacking purplish veins; keel tip various, but not as above; legume unilocular or bilocular, ascending or spreading; leaflets less than three times longer than broad 10
10. Flowers commonly less than 12 mm long; pods bilocular, ovoid-inflated, membranous, spreading 8. *A. lentiginosus*
10. Flowers more than 12 mm long; pods unilocular, oblong-subcylindric, leathery, erect-ascending 11. *A. terminalis*

1. *Astragalus agrestis* Dougl. ex Hook. Commonly on clay soil of the plains and up in the mountains. Idaho, north to Manitoba and the Yukon, south to California and New Mexico. Birch Creek, Clark Co., 25 June 1967, 1127.

2. *Astragalus calycosus* Torr. ex Wats. Sagebrush to dry open slopes, May to July. Central Idaho to Wyoming, south to California, Arizona and New Mexico. Six miles southwest of Atomic City, Bingham Co., 26 May 1967, 864. R.28E., T.4N., Butte Co., 12 June 1967, 953.

3. *Astragalus canadensis* L. var. *brevidens* (Grandg.) Barn. From moist areas to alkaline flat, June to July. Idaho, west to California, north and east to British Columbia to the Atlantic Coast, and from the Great Plains to Texas. T.6N., R.31E., Butte Co., 8 June 1967, 906.

4. *Astragalus ceramicus* Sheld. Mostly in sandy areas, May to July. Central Idaho to eastern Montana, the Dakotas and Nebraska, south to Arizona. T.6N., R.31E., Butte Co., 8 June 1967, 911. R.34E., T.5N., Jefferson Co., 20 June 1967, 993.

5. *Astragalus cibarius* Sheld. Sagebrush plains, May to June. Central Idaho, north to Montana, south to Nevada, Utah, Colorado, and New Mexico. R.28E., T.4N., Butte Co., 20 May 1967, 792.

6. *Astragalus curvicaupus* (A. Hell.) Macbr. var. *curvicaupus*. Sagebrush plains, May to July. Idaho, west to Oregon, south to Nevada and California. Middle Butte, Bingham Co., 6 May 1967, 884.

7. *Astragalus filipes* Torr. Sagebrush slopes, May to June. Idaho, north and west from British Columbia to California and Nevada. Big Lost River Bridge, Butte Co., 6 June 1967, 885.

8. *Astragalus lentiginosus* Dougl. ex Hook. var. *salinus* (Howell) Barn. Desert alkaline flats to middle elevations in the mountains. T.6N., R.31E., Butte

Co., 8 June 1967, 910.

9. *Astragalus miser* Dougl. ex Hook. var. *praeteritus* Barn. From dry ground at lower elevations to moist meadows in the mountains, May to July. Central Idaho, south to Wyoming, west to Montana. East Butte, Bingham Co., 22 June 1967, 1016. T.4N., R.28E., Butte Co., 13 June 1967, 980.

10. *Astragalus purshii* Dougl. ex Hook. var. *purshii*. Sagebrush plains to the lower foothills in the mountains, April to June. Idaho, north and west from British Columbia to California, east to Alberta, the Dakotas, and Colorado. Big Lost River Bridge, Butte Co., 6 June 1967, 897.

10a. *Astragalus purshii* Dougl. ex Hook. var. *concinus* Barn. On the plains, from central Idaho to west central Montana. Six miles east of Arco, Butte Co., 13 May 1933, Davis s.n., (IDS).

11. *Astragalus terminalis* Wats. Common in sagebrush, May to June. Central Idaho to Montana, east to Wyoming. T.4N., R.28E., Butte Co., 12 June 1967, 956.

2. *Glycyrrhiza* L. Licorice

1. *Glycyrrhiza lepidota* Pursh. Common along streams and in waste places, May to August. British Columbia to Ontario, south to New York, New Mexico, and California. Big Lost River, Butte Co., 29 July 1967, 1188.

3. *Hedysarum* L.

1. *Hedysarum boreale* Nutt. Dry plains, May to August. Saskatchewan to central Idaho, south to New Mexico and Arizona. R.31E., T.6N., Butte Co., 8 June 1967, 914.

4. *Lupinus* L. Lupine

1. Plants annual 4. *L. pusillus*

1. Plants perennial 2

2. Leaves mostly cauline; plants erect with a well branched crown 1. *L. argenteus*

2. Leaves basal and cauline 3

3. Plants low and spreading to matted 2. *L. lepidus*

3. Plants erect, cauline leaves with petioles to 20 cm long 4

4. Leaflets pubescent on the upper surface, acuminate to apiculate; flowers bluish to violet or white in our area 3. *L. prunophilus*

4. Leaflets glabrous on the upper surface, usually rounded or acute; flowers deep violet to purple 5. *L. wyethii*

1. *Lupinus argenteus* Pursh subsp. *argenteus* var. *tenellus* (Dougl. in G. Don) Dunn. Central Idaho to central Montana, Wyoming and Utah, May to July. Big Butte, Butte Co., 26 May 1967, 869.

2. *Lupinus lepidus* Dougl. ex Lindl. Dry plains and slopes, June to August. California to British Columbia, east to Montana, Wyoming and Colorado.

Five miles west of Arco, Butte Co., 14 May 1939, O. Mays, s.n., (IDS).

3. *Lupinus x prunophilus* M. E. Jones. Plains and foothills, May to June. Central and eastern Washington, northeastern Oregon, southcentral Idaho, south to Nevada, Utah, and Colorado. Webb Springs, Butte Co., 24 May 1967, 840.

4. *Lupinus pusillus* Pursh. Mostly in sandy soil, May to June. Idaho, west to Washington, south to California, east to Alberta to Nebraska. Webb Springs, Butte Co., 24 May 1967, 838.

5. *Lupinus wyethii* Wats. Open ridges and forests to sagebrush plains, May to July. Idaho, west from British Columbia to California, east from Alberta to Colorado. Big Lost River Bridge, Butte Co., 6 June 1967, 886.

5. Medicago L.

1. *Medicago sativa* L. Native to the Old World. Often escaping from cultivation, June to October. Camas Creek, Jefferson Co., 1 September 1955, French, 23, (NRTS).

6. Melilotus Mill. Sweet clover

1. *Melilotus officinalis* (L.) Lam. Native of the Mediterranean area, a weedy plant in our area. May to September. Sec. 3, T.6N., R.33E., Jefferson Co., 7 June 1956, McBride, 120, (NRTS).

7. Oxytropis DC. Stemless loco

1. Corolla purple to reddish-purple; pubescence sericeous-silky; leaves 3 to 7 cm long; leaflets 7 to 15 mm long; pods 1.5 cm long 1. *O. lagopus*

1. Corolla white to yellow; pubescence densely grayish villous to strigose; leaves 5 to 30 cm long; leaflets 1-3.5 cm long; pods 1.5-2.5 cm long 2. *O. sericea*

1. *Oxytropis lagopus* Nutt. var. *lagopus*. Plains and lower mountains, May to June. Idaho and Montana. R.28E., T.4N., Butte Co., 12 June 1967, 950.

2. *Oxytropis sericea* Nutt. var. *sericea*. Middle elevations to the plains, May to July. Western Montana to northeastern Nevada, New Mexico, and Texas. R.31E., T.3N., Bingham Co., 24 May 1967, 856.

8. Petalostemon Michx. Prairie clover

1. *Petalostemon ornatum* Dougl. ex Hook. Commonly in sagebrush, sandy or rocky soil, May to July. South and central Idaho, west to Washington and Oregon. Sec. 9, T.3N., R.30E., Butte Co., 26 June 1957, Goodwin, 131, (NRTS).

9. Psoralea L.

1. *Psoralea lanceolata* Pursh. Mostly in sandy soil, May to September. Idaho, west from Washington to Nevada, east to Nebraska. R.34E., T.5N., Jefferson

Co., 20 June 1967, 996. R.31E., T.6N., Butte Co., 18 July 1967, 1167.

10. Thermopsis R. Br. Buck-bean

1. *Thermopsis montana* Nutt. Mostly along streams or moist places, May to August. Idaho, west from British Columbia to California, east from Montana to Colorado and Utah. Birch Creek, Clark Co., 25 June 1967, 1044.

11. Vicia L. Vetch

1. *Vicia sativa* L. Introduced from Europe and now widespread in the United States, May to July. R.31E., T.6N., Butte Co., 8 June 1967, 907.

LINACEAE, FLAX FAMILY

1. Linum L. Flax

1. *Linum perenne* L. Mostly in dry areas, May to July. Over much of western North America; Eurasia. North of junction 22-28, Clark Co., 24 June 1967, 1060.

LOASACEAE. BLAZING-STAR FAMILY

1. Mentzelia L. Blazing star

1. Annual plants 1 to 4 dm tall; petals 1.5 cm long 1. *M. albicaulis*

1. Biennial plants 3 to 10 dm tall; petals 1.5-8 cm long 2. *M. laevicaulis*

1. *Mentzelia albicaulis* Dougl. ex Hook. Desert plains, in sandy soil. May to July. Idaho, west from British Columbia to California, east to Montana to New Mexico. Cave by EBR.II Reactor, Butte Co., 18 May 1967, 769.

2. *Mentzelia laevicaulis* (Dougl.) T. & G. Desert and mountains, July to September. Idaho, west from British Columbia to California, east to Wyoming. Arco desert, Butte Co., June 1950, Davis, 183, (IDS).

MALVACEAE. MALLOW FAMILY

1. Sphaeralcea St. Hil.

1. Leaves crenate or if lobed less than halfway to the midrib; calyx bracteolate 2. *S. munroana*

1. Leaves divided almost to the midrib; calyx tribracteolate 1. *S. grossulariaefolia*

1. *Sphaeralcea grossulariaefolia* (H. & A.) Rydb. Mostly on dry soil, June to July. Central Idaho, west from Washington to Nevada and Utah. Big Lost River, Butte Co., 1 July 1967, 1094.

2. *Sphaeralcea munroana* (Dougl.) Spach. ex Gray. Dry plains and mountains, May to August. Idaho, west and south from British Columbia, to Cali-

fornia and Utah. T.4N., R.30E., Butte Co., 1 June 1953, McBride, s.n., (UTC).

NYCTAGINACEAE. FOUR-O'CLOCK FAMILY

1. *Abronia* Juss. Sand verbena

1. *Abronia mellifera* Dougl. ex Hook. Dunes and sandy soil, May to July. Columbia River Gorge, east to central and southeastern Washington and adjacent Oregon, east to eastern Idaho. R.31E., T.6N., Butte Co., 9 June 1967, 916.

ONAGRACEAE. EVENING PRIMROSE FAMILY

1. Seeds with a tuft of hairs (coma) at the tip; leaves usually opposite 2. *Epilobium*
1. Seeds without coma; leaves mostly alternate ... 2
2. Ovary 2-loculed 3. *Gayophytum*
2. Ovary 4-loculed 3
3. Stigma 4-lobed 4. *Oenothera*
3. Stigma capitate 1. *Camissonia*

1. *Camissonia* Link.

1. Petals yellow; capsule sessile, straight, fusiform, crowded 1. *C. andina*
1. Petals white, often reddish; capsule sessile, often contorted 2. *C. minor*
1. *Camissonia andina* (Nutt.) Raven. Dry soil, May to June. Desert near Big Butte, Butte Co., 17 May 1938, Davis, 139, (IDS).
2. *Camissonia minor* (Nels.) Raven. Dry soil, May to June. Near Big Butte, Butte Co., 28 June 1950, AEC Project, 164 (IDS).

2. *Epilobium* L. Willow herb

1. *Epilobium watsonii* Barn. var. *parishii* (Trel.) Hitchc. Commonly in moist places, June to September. Spreading throughout the United States. Birch Creek, Clark Co., 5 September 1967, 1219.

3. *Gayophytum* Juss

1. Plants usually branched from the base; capsules nearly sessile; petals 1 mm long or less 2. *G. racemosum*
1. Plants usually branched from above; capsules pedicelled; petals 1 to 5 mm long 1. *G. nuttallii*
1. *Gayophytum nuttallii* T. & G. Dry sandy and gravelly soil of the plains and foothills, June to August. Common in the western states. Shell road, Butte Co., 23 May 1967, 836. Our plants belong to variety *diffusum* and *villosum* and are quite distinctive in this area.
2. *Gayophytum racemosum* T. & G. Lower desert plains to well up in the mountains, May to July. Washington to California, east from Montana to Colorado and Utah. T.4N., R.31E., Butte Co., 20 May 1967, 781.

4. *Oenothera* L. Evening Primrose

1. Plants with leafy flowering stems 2
1. Plants without leafy flowering stems 4
2. Petals large, over 1 cm long, white or pink 3. *O. pallida*
2. Petals smaller, less than 1 cm long or yellow ... 3
3. Plants annual, 1 to 5 dm tall; stigmatic lobes less than 5 mm long 4. *O. scapoidea*
3. Plants biennial or perennial, mostly over 5 dm tall (up to 5 m); stigmatic lobes about 5 mm long 2. *O. hookeri*
4. Leaf margins ciliate; capsules short-pedicellate 1a. *O. caespitosa* var. *marginata*
4. Leaf margins not ciliate; capsules sessile 1b. *O. caespitosa* var. *montana*
- 1a. *Oenothera caespitosa* Nutt. var. *marginata* (Nutt.) Munz. Commonly of dry, rocky soil in the plains, May to July. Idaho, west to California, south to Colorado and Utah. West of Big Lost River Bridge, Butte Co., 13 July 1967, 880.
- 1b. *Oenothera caespitosa* Nutt. var. *montana* (Nutt.) Durand. Washington, Oregon and Idaho. East Butte, Bingham Co., 22 June 1967, 1007. T.4N., R.31E., Butte Co., 20 May 1967, 784.
2. *Oenothera hookeri* T. & G. In moist areas of the plains and lower mountain streams, June to September. Central Idaho, west to Washington, Oregon, and California, south to Utah, New Mexico, east to Texas. Big Lost River, Butte Co., 13 July 1967, 1142.
3. *Oenothera pallida* Lindl. Mostly in hot, dry sandy soil, May to July. Idaho, west to Washington and Oregon, south to Arizona and New Mexico. EBR. II Reactor, Butte Co., 3 July 1967, 1115.
4. *Oenothera scapoidea* Nutt. in T. & G. Commonly in sagebrush and sandy soil, May to July. Central Idaho, west to Oregon, south to Wyoming, Colorado, and Utah. Shell Road, Butte Co., 8 June 1967, 922.

OROBANCHACEAE. BROOMRAPE FAMILY

1. *Orobanche* L. Broomrape; Cancerroot

1. Flowers long-pedicellate, without bractlets; corolla equally 5-cleft 1. *O. fasciculata*
1. Flowers sessile or pedicels less than 3 mm long with a pair of bractlets beneath the calyx; calyx unequally 5-cleft 2. *O. grayana*
1. *Orobanche fasciculata* Nutt. Foothills and plains, May to July. Michigan to British Columbia, south to Texas and California. Tractor Flat, Jefferson Co., 20 June 1967, 995.
2. *Orobanche grayana* Beck. British Columbia, south to California and Nevada, June to September. Six miles southwest of Atomic City, Butte Co., 18 July 1967, 1162.

PLANTAGINACEAE. PLAINTAIN FAMILY

1. *Plantago* L. Plaintain

1. Small annual plants; leaves small, linear to narrowly lanceolate; seeds 2 per capsule 2. *P. purshii*
1. Perennial plants; leaves broad, large; seeds 6 to 30 per capsule 1. *P. major*
1. *Plantago major* L. A weedy species, May to September. Cosmopolitan. Birch Creek, Clark Co., 5 September 1967, 1220.
2. *Plantago purshii* R. & S. Dry soil. Ontario to British Columbia, south to Texas and California. R.29E., T.3N., Butte Co., 1 July 1967, 1095.

POLEMONIACEAE. PHLOX FAMILY

1. Cauline leaves lacking, represented only by the persistent cotyledons and basally connate bracts; small annuals 4. *Gymnosteris*
1. Cauline leaves more or less well developed; annual or perennial plants 2
2. Calyx-tube tending to remain unbroken to maturity of the capsule; leaves prevailingly alternate, at least above. 3
2. Calyx-tube tending to split along intercostal membranes 4
3. Stamens unequally inserted on the corolla tube; calyx enlarging in fruit 1. *Collomia*
3. Stamens more or less equally inserted close to the sinuses of the corolla; calyx not enlarging in fruit 7. *Navarretia*
4. Leaves entire, mostly opposite; filaments very unequally inserted 8. *Phlox*
4. Leaves dissected or lobed; filaments more or less equally inserted 5
5. Annuals with the flowers borne in leafy-bracteate, tomentose heads; anthers deeply sagittate 2. *Eriastrum*
5. Perennials or if annual the flowers not in heads 6
6. Leaves sessile, palmatifid or pinnatifid; shrubby pungent plants 6. *Leptodactylon*
6. Leaves not sessile and palmatifid, principal leaves alternate, pinnately lobed to entire 7
7. Leaf lobes setose (spine-tipped); sepals unequal 5. *Langloisia*
7. Leaf lobes usually not spine-tipped; sepals equal or subequal 3. *Gilia*

1. *Collomia* Nutt.

1. Plants 1 to 6 dm tall, unbranched; filaments unequally inserted 1. *C. linearis*
1. Plants 1 to 2 dm tall, freely branched; filaments equally inserted 2. *C. tenella*
1. *Collomia linearis* Nutt. Dry to moist habitats, May to August. Common in western North America moving eastward. Webb Springs, Butte Co., 1 July 1970.

2. *Collomia tenella* Gray. Common in sagebrush and open places, June to July. Central Idaho, west to Washington and Oregon, east to Wyoming, south to Utah and Nevada. Webb Springs, Butte Co., 1 July 1967, 1072.

2. *Eriastrum* Woot. & Standl.

1. *Eriastrum sparsiflorum* (Eastw.) Mason var. *wilcoxii* (A. Nels.) Cronq. Desert plains, often in sand, May to August. Idaho, west to California, south to Utah. EBR. II Reactor, Bingham Co., 3 July 1967, 1113.

3. *Gilia* R. & P.

1. Plants biennial or perennial 2
1. Plants annual 3
2. Corolla red; stems mostly over 2 dm tall 1. *G. aggregata*
2. Corolla white, stems mostly 2 dm or less tall 2. *G. congesta*
3. Leaves usually entire, basal and stem leaves present 4
3. Leaves toothed to pinnatifid, mostly basal; corolla 1.5-4 mm long 5. *G. tenerrima*
4. Leaves toothed or lobed; seeds mostly 8 to 12 per locule, less than 1 mm long 3. *G. leptomeria*
4. Leaves usually pinnatifid; seeds 2 to 8 per locule, 1.5 mm long 4. *G. sinuata*
1. *Gilia aggregata* (Pursh) Spreng. Rocky, open ground of the plains to middle elevations, May to August. British Columbia to Idaho, east to Colorado, south to Mexico. Southwest of Howe, Butte Co., 12 June 1967, 954.
2. *Gilia congesta* Hook. Dry rocky ground at lower elevations to higher in the mountains, June to August. Idaho, west to Oregon and California, east to North Dakota, Nebraska and Colorado. R.31E., T.6N, Butte Co., 8 June 1967, 905.

3. *Gilia leptomeria* Gray. Mostly in sandy soil of the plains, May to July. Idaho, west from Washington to California, south to Colorado to New Mexico. Webb Springs, Butte Co., 24 May 1967, 839. R.34E., T.5N., Jefferson Co., 20 June 1967, 989.

4. *Gilia sinuata* Dougl. ex Benth. Mostly of the plains, May to July. Idaho, west from Washington to California, east to Wyoming, south to New Mexico. T.6N., R.30E., Butte Co., 18 May 1967, 759.

5. *Gilia tenerrima* Gray. Plains to middle elevations, June to August. Central Idaho and Montana, west to Oregon, south to Wyoming, Colorado, and Utah. Six miles west of Atomic City, Butte Co., 1 July 1967, 1164.

4. *Gymnosteris* Greene

1. *Gymnosteris nudicaule* (H. & A.) Greer sandy places, April to May. Baker County and the Snake River Plains south to Nev

toward Arco, Butte Co., 13 May 1933, Davis, s.n., (IDS).

5. *Langloisia* Greene

1. *Langloisia setosissima* (T. & G.) Greene. Commonly in sandy soil of the plains, May to July. Oregon, south to California, east and south from Idaho to Mexico. T.6N., R.30E., Butte Co., 6 June 1967, 899.

6. *Leptodactylon* H. & A.

1. Plants diffusely branched, up to 30 cm tall; leaves predominately alternate

. 1. *L. pungens*

1. Plants only moderately branched, up to 15 cm tall; leaves predominately opposite

. 2. *L. watsonii*

1. *Leptodactylon pungens* (Torr.) Rydb. Rocky or sandy soil of the plains and desert, May to July. British Columbia to California, east to Montana, Nebraska, south to New Mexico. Shell Road, Butte Co., 23 May 1967, 835.

2. *Leptodactylon watsonii* (Gray) Rydb. Common on rocky ledges and gravelly soil, June to July. Idaho, Colorado, and Utah. R.28E., T.4N., Butte Co., 22

7. *Navarretia* R. & P.

1. *Navarretia breweri* (Gray) Greene. Dry or moist ground, commonly as understory, May to July. Central Idaho, west to Washington to California, east from Wyoming to Arizona. Big Butte Canyon, Butte Co., 1 July 1967, 1108.

8. *Phlox* L. *Phlox*

1. Caespitose, glandular to hirsute plants not especially mat forming; leaves firm, mostly over 1 cm long; style over 5 mm long 2

1. Mat forming, arachnoid plants; leaves firm and pungent, mostly 0.5-1 cm long; flowers mostly sessile; style 2 to 5 mm long 2. *P. hoodii*

2. Flowers with long pedicels; style 6 to 15 mm long; plant with well developed internodes

. 3. *P. longifolia*

2. Flowers short-pedicellate; style 5 to 10 mm long; plant with short internodes 1. *P. aculeata*

1. *Phlox aculeata* A. Nels. Commonly in sagebrush, alkaline, or sandy clay soil, April to May. Snake River Plains, west to Oregon. East Butte, Bingham Co., 18 May 1967, 773. T.4N., R.28E., Butte Co., 20 May 1967, 695.

2. *Phlox hoodii* Rich. Dry, rocky plains and foothills, April to June. Common through the western states and southern Canada. R.28+, T.4N., 20 May 1967, 789.

3. *Phlox longifolia* Nutt. Dry, rocky places, April to July. British Columbia to Montana, south to California, Wyoming, Colorado, and New Mexico. Bit Butte, Butte Co., 20 June 1950, AEC, 15, (IDS).

POLYGONACEAE. BUCKWHEAT FAMILY

1. Leaves without sheathing stipules; stamens mostly 9 2

1. Leaves with sheathing stipules; stamens 4 to 8 3

2. Involucre with 3 to 6 spine-tipped teeth or lobes 2. *Oxytheca*

2. Involucre with 3 to 10 nonspiny teeth or lobes 1. *Eriogonum*

3. Perianth segments mostly 5 (sometimes 4 or 6), never with grainlike callosities, stigma capitate 3. *Polygonum*

3. Perianth segments usually 6 (sometimes 4), 1 or more often with a grainlike callosity; stigmas tufted 4. *Rumex*

1. *Eriogonum* Michx.

1. Annual plants 2

1. Perennial plants 3

2. Involucres sessile, spicate, mostly single at the dichotomies and along the unbranched stem tips, not reflexed 7. *E. vimineum*

2. Involucres with reflexed peduncles; leaves all basal 2. *E. cernuum*

3. Perianth narrowed to a slender stipelike base which is jointed to the pedicel 4

3. Perianth rounded to acute at base, narrowed to the point of attachment (joint) with the pedicel but without a slender stikelike base 5

4. Flowering stems with a whorl of leaves (bracts) about midlength; plants erect and well over 10 cm tall (1-4 dm tall) 3. *E. heracleoides*

4. Flowering stems without a whorl of leaves (bracts) about midlength; plants low and spreading, 10 cm or less tall 1. *E. caespitosum*

5. Plants matforming; involucres often capitate or umbellate 6

5. Plants not matforming; involucres borne in broad, compound, cymose inflorescences 5. *E. microthecum*

6. Perianth segmented for 2/3 to 3/4 or its length; pale grayish-lanate throughout 4. *E. mancum*

6. Perianth segmented nearly to the swollen basal joint; from pannose-lanate and almost white on both surfaces to less tomentose, sometimes greenish above 6. *E. ovalifolium*

1. *Eriogonum caespitosum* Nutt. Sagebrush flat, grassy hills and pinyon-juniper lands, April to July. Eastern California and Oregon, eastward to Montana, Idaho, Wyoming, and Colorado. Lava beds, Bingham Co., 27 May 1969, E.C. Moran, s.n., (BRY).

2. *Eriogonum cernuum* Nutt. var. *cernuum*. In the hills and valleys of the plains, June to August. South central Oregon to southeastern California, east across southern Idaho to eastern Montana, Nebraska, Colorado, and New Mexico. By ERB. II Reactor, Bingham Co., 3 July 1967, 1114.

3. *Eriogonum heracleoides* Nutt. var. *Hera-
cleoides*. Gravelly to loamy soil in the desert and
rocky ridges to about 6,000 feet, May to August.
Utah, Nevada, Wyoming, east to western Montana,
northeastern California, and British Columbia. East
Butte, Bingham Co., 22 June 1967, 1021.

4. *Eriogonum mancum* Rydb. Sagebrush flats and
grassy hills, June to July. Granite and Powell Coun-
ties Montana, south to Lehmi and Clark Co., Idaho.
Birch Creek, Clark Co., 25 June 1967, 1057.

5. *Eriogonum microthecum* Nutt. var. *laxiflorum*
Hook. Sandy deserts and low mountain slopes, June
to August. Washington and California, east to Mon-
tana, Nebraska, Arizona, New Mexico and Colorado.
South of Junction 88-Lincoln Blvd., Butte Co., 24
August 1967, 1202.

6. *Eriogonum ovalifolium* Nutt. var. *ovalifolium*.
From sagebrush slopes to above timberline, May to
August. British Columbia, south through Washington,
western Oregon, and California, on the eastern side of
the Rocky Mountains. T.4N., R.28E., Butte Co., 21
May 1967, 802. T.6N., R.30E., Butte Co., 6 June
1967, 900.

7. *Eriogonum vimineum* Dougl. in Benth. Pine
woodlands, to sagebrush and desert lands in sandy or
rocky soil, June to September. Washington and Ida-
ho, southward through Oregon into northwestern
Nevada and central California. Should be looked for
on the site.

2. *Oxytheca* Nutt.

1. *Oxytheca dendroidea* Nutt. var. *dendroidea*.
Common in sagebrush, June to August. Central Wash-
ington, Oregon, south to California, east to Idaho and
Nevada; Chile and Argentina. T.3N., R.30E., Butte
Co., 25 June 1956, McBride, 105, (NRTS).

3. *Polygonum* L. Knotweed

- 1. Perianth undivided except for a short limb;
plants fragile 2. *P. polycenocoides*
- 1. Perianth divided at least to the middle; plants not
fragile 2
- 2. Calyx lobes yellowish; plants erect, 1 m tall
..... 3. *P. ramissimum*
- 2. Calyx lobes white or pinkish margined; plants
prostrate to ascending, 1 to 4 dm tall
..... 1. *P. achoreum*

1. *Polygonum achoreum* Blake. Dry waste ground,
July to September. Eastern Oregon and Montana,
south to Idaho and Colorado, east to Canada and nor-
thern United States to Quebec and New York. S.W.
of Big Butte, Butte Co., 27 June 1950, AEC, 144,
(IDS).

2. *Polygonum polyceneoides* Juab. & Spach.
Growing in sandy areas. New York and south central
Idaho; Asia, June to August. East of Jct. 88-Lincoln
Blvd., 24 August 1967, 1207.

3. *Polygonum ramosissimum* Michx. Moist to dry
wasteground, July to September. In most of the
United States, except the S.E.; over most of southern
Canada. Webb Springs, Butte Co., 13 June 1967, 970.

4. *Rumex* L. Dock

- 1. Flowers mostly imperfect; leaves hastate
..... 1. *R. acetosella*
- 1. Flowers perfect; leaves not hastate 2
- 2. Plant rhizomatous, leaves leathery
..... 4. *R. venosus*
- 2. Plant with a strong taproot; leaves various 3
- 3. Leaf margins crisped; petioles usually papillose-
puberulent 2. *R. crispus*
- 3. Leaf margins plane to undulate, but not crisped;
petioles glabrous 3. *R. salicifolius*
- 1. *Rumex acetosella* L. A very weedy plant, May
to August. Native of Europe and now over most of
the world. Desert, Butte Co., 1950, AEC, 37A, (IDS).
- 2. *Rumex crispus* L. A weed of fields and waste
places, generally in moist areas, June to September.
Over most of the United States; Europe. Webb
Springs, Butte Co., 1 July 1967, 1066. Flood Control
area, Butte Co., 1 July 1967, 1096.
- 3. *Rumex salicifolius* Weinm. Sandy and moist
areas in the plains and mountains, June to September.
Alaska to California, east to Nebraska and Texas, and
in Canada and northern U.S. to Quebec, south to
New York; Europe. Big Butte, Butte Co., June 1950;
AEC, 128, (IDS).
- 4. *Rumex venosus* Pursh. Dry sandy soil, April to
June. Alberta to Washington, California, east to
Texas. T.4N., R.28E., Butte Co., 21 May 1967, 883.

RANUNCULACEAE. BUTTERCUP FAMILY

- 1. Flowers irregular; upper sepal spurred
..... 2. *Delphinium*
- 1. Flowers more or less regular; upper sepal not
spurred, petals may be spurred 2
- 2. Petals spurred; fruit of follicles 1. *Aquilegia*
- 2. Petals not spurred; fruit of achenes
..... 3. *Ranunculus*

1. *Aquilegia* L. Columbine

1. *Aquilegia formosa* Fisch. Moist mountains,
meadows, and slopes, May to August. Widely dis-
tributed in western North America. Webb springs, 1
July, 1080. Birch Creek, Clark Co., 25 June 1967,
1041.

2. *Delphinium* L. Larkspur

- 1. Stems 1-several, commonly over 4 dm tall, from
a very fibrous root system 1. *D. andersonii*
- 1. Stems usually single, usually less than 4 dm tall,
from a tuberous root system 2. *D. menziesii*
- 1. *Delphinium andersonii* Gray. Commonly in
sagebrush and juniper of desert ranges, April to June.

California, Nevada and south central Idaho. South slope of Middle Butte, Bingham Co., 22 June 1967, 1029.

2. *Delphinium menziesii* DC. subsp. *utahense* (Wats.) D. Sutherland. Prairies, canyons, and lower montane meadows. British Columbia, south to California and Utah, April to June. R.28+, T.4N., Butte Co., 21 May 1967, 812.

3. *Ranunculus* L. Buttercup; Crowfoot

1. Plants not both scapose and perennial; achenes strongly compressed 2

1. Perennial scapose plants; achenes not strongly compressed 1. *R. andersonii*

2. Low annual plants, 7 mm, or less high, appearing early in the spring; achenes woolly, usually densely so 4. *R. testiculatus*

2. Mostly perennial plants (in ours), over 7 cm tall; achenes not woolly 3

3. Receptacle globose; achenes each with a broad thin wing or stipe at base 2. *R. glaberrimus*

3. Receptacle ellipsoid; achenes not stipitate or winged at base 3. *R. macounii*

1. *Ranunculus andersonii* Gray. Sagebrush and juniper-pinyon hills, April to June. California, south to Nevada, north to eastern Oregon and central Idaho. North of Middle Butte, Bingham Co., 21 April 1967, 752.

2. *Ranunculus glaberrimus* Hook. var. *ellipticus* Greene. Sagebrush and grassland valleys, March to June. California, to British Columbia, east to North and South Dakota, Nebraska, and New Mexico. T.1N., R.30E., Butte Co., 22 May 1967; 823.

3. *Ranunculus macounii* Britt. var. *macounii*. Usually in damp places at low elevations, May to July. Northern California, north to British Columbia and Alberta, south to Arizona and New Mexico, east to Labrador, Michigan to Nebraska. Birch Creek, Clark Co., 25 June 1967, 1050.

4. *Ranunculus testiculatus* Crantz. Commonly in sagebrush areas, March to May. Oregon and eastern Washington, east to Idaho and Colorado, south to Nevada. North base of East Butte, Bingham Co., 18 May 1967, 775.

RHAMNACEAE. BUCKTHORN FAMILY

1. *Ceanothus* L.

1. *Ceanothus velutinus* Dougl. ex. Hook. var. *velutinus*. Moist areas in the mountains, June to August. Idaho, west from British Columbia to Nevada, east to Montana, South Dakota and Colorado. Big Butte, Butte Co., 1 July 1967, 1101.

ROSACEAE. ROSE FAMILY

1. Plants bearing prickles; leaves pinnate; carpels several 9. *Rosa*

1. Plants not with the above combination of characters 2

2. Ovary more or less inferior, compound, 2 to 5-locular; fruit a pome 1. *Amelanchier*

2. Ovary superior, with a single carpel; fruit of achenes, follicles, drupes, or drupelets 3

3. Fruit a fleshy, 1-seeded drupe; pistil 1; leaves simple 7. *Prunus*

3. Pistils 1 to several, if 1 then not drupaceous; leaves simple, compound or persistent 4

4. Petals lacking; pistil 1, developing into an achene; style plumose; leaves simple 2. *Cercocarpus*

4. Petals present; pistils usually more than 1, if 1 then without a plumose style; leaves simple or compound 5

5. Leaves compound with 3 or more leaflets 6

5. Leaves simple or deeply lobed, but not compound 8

6. Petals bright yellow; fruit of dry achenes 6. *Potentilla*

6. Petals white; fruit of follicles or drupelets 7

7. Plants with bristles or prickles; fruit fleshy, of drupelets 10. *Rubus*

7. Plants without bristles or prickles; fruit of follicles 3. *Chamaebatiaria*

8. Leaves entire, not lobed 4. *Holodiscus*

8. Leaves toothed to shallowly lobed 9

9. Leaves deeply 3-toothed at the tip only, small, revolute-margined; pistils solitary; fruit an achene 8. *Purshia*

9. Leaves usually 3 to 5-palmately lobed, larger, not revolute-margined; pistils 1 to 5; fruit a follicle 5. *Physocarpus*

1. *Amelanchier* Medic. Serviceberry

1. *Amelanchier utahensis* Koehne. Commonly in sagebrush deserts to well up in the mountains, May to June. Central Idaho, west to California and Oregon, east to southern Montana, Wyoming, Colorado, New Mexico and Texas. East Butte, Bingham Co., 22 June 1967, 1023. Webb Springs, Butte Co., 26 May 1967, 870.

2. *Cercocarpus* HBK Mountain Mohogany

1. *Cercocarpus ledifolius* Nutt. in T. & G. Lower foothills to rocky mountain ridges, April to June. Montana, southwest to Washington, Oregon, California and Arizona, west to Colorado and Utah. R.28E., T.4N., Butte Co., 21 May 1967, 803.

3. *Chamaebatiaria* (Porter) Maxim. Fern Bush

1. *Chamaebatiaria millefolium* (Torr.) Maxim. Desert plains and foothills, commonly in lava in our area. June to August. Oregon, south to Nevada and California, Arizona, east through central Idaho to Utah. R.29E., T.7N., Butte Co., 10 June 1967, 1165b.

4. *Holodiscus* Maxim. Mountain Spray

1. *Holodiscus dumosus* (Hook.) Heller. Rocky soil

of the plains to moist areas in the mountains, June to August. Oregon, south to California, east and south to central Idaho, Wyoming, Colorado, New Mexico, Utah, Arizona, and Nevada. East Butte, Bingham Co., 22 June 1967, 1014. Webb Springs, Butte Co., 13 June 1967, 973.

5. *Physocarpus Maxim.* Nine Bark

1. *Physocarpus alternans* (Jones) Howell. Dry rocky slopes at low elevations. Central Idaho, south to Utah and Nevada. R.29E., T.7N., Butte Co., 10 June 1967, 926. Should be looked for at the NRTS.

6. *Potentilla L.* Cinquefoil

- 1. Stamens 10 to 20; style terminal 2
- 1. Stamens more than 20; style lateral 3
- 2. Lower portion of the stems hirsute; stamens mostly over 15 4. *P. norvegica*
- 2. Lower portions of the stems soft pubescent; stamens 10 or 15 2. *P. biennis*
- 3. Stems creeping (stoloniferous) and rooting; flowers solitary; pubescence grayish, silky-tomentose 1. *P. anserina*
- 3. Stems erect, not rooting; flowers in terminal cymes; pubescence glandular-puberulent to pilose-glandular 3. *P. glandulosa*

1. *Potentilla anserina* L. Moist areas of the plains and meadowlands, May to August. Atlantic coast, west to California. Flood Control Area, Butte Co., 1 July 1967, 1098.

2. *Potentilla biennis* Greene. Moist shady areas at lower elevations to higher up in the mountains, May to August. Idaho, west to Washington, north and south from Saskatchewan to Colorado. Big Lost River, Butte Co., 13 July 1967, 1145.

3. *Potentilla glandulosa* Lindl. var. *glandulosa*. Moist soil in the plains to middle elevations, May to July. Washington, Idaho, and Oregon. Big Butte Canyon, Butte Co., 1 July 1967, 1100.

4. *Potentilla norvegica* L. A weed in the eastern United States, now over much of North America. May to August. Flood Control Area, Butte Co., 1 July 1967, 1097.

7. *Prunus L.* Cherry

1. *Prunus virginiana* L. Variable in habitat from the lower grassland and sagebrush plains to well up in the mountains, May to July. Webb Springs, Butte Co., 1 July 1967, 1064.

8. *Purshia DC. ex Poir* Bitter Brush

1. *Purshia tridentata* (Pursh) DC. Commonly from sagebrush to wooded areas, April to June. Idaho, north and west from British Columbia to Nevada and California, east to Montana, Wyoming, Utah, and New Mexico. Six miles south west of Atomic City, Bingham Co., 22 May 1967, 865. Big Butte Co., 20 June 1950, AEC, 16, (IDS).

9. *Rosa L.* Rose

1. *Rosa woodsii* Lindl. Commonly along streambanks or moist areas, May to July. Idaho, west to Oregon, Washington, and California, east to Minnesota and to Texas. Big Butte, Butte Co., 22 June 1950, AEC, 89, (IDS).

10. *Rubus L.* Blackberry; Raspberry

1. *Rubus ideaus* L. Streambanks to moist woods, May to July. Over much of North America; Asia. Big Butte, Butte Co., 1 July 1967, 1101.

RUBIACEAE. MADDER FAMILY

1. *Galium L.* Bedstraw, Cleavers

1. Plants perennial from creeping rhizomes; leaves mostly in whorles of 4; fruit without ucnate hairs (may be flexuous) 2. *G. multiflorum*

1. Plants annual from a taproot; leaves 2 to 4 in a whorle; fruit with ucnate hairs . . 1. *G. bifolium*

1. *Galium bifolium* Wats. Often as understory in dry to moist places, May to August. British Columbia and Montana, south to California and Colorado. Big Butte, Butte Co., 27 June 1950, AEC, 120, (IDS).

2. *Galium multiflorum* Kell. Desert plains and rocky slopes, May to August. Central Idaho, west from Washington to California, south to Utah, and Arizona. Webb Springs, Butte Co., 13 June 1967, 968.

SALIACEAE. WILLOW FAMILY

1. Buds with several scales; stamens numerous; flowers borne on a cuplike disk 1. *Populus*

1. Buds with a single scale; stamens commonly 1 to 2 or many; flowers without disks 2. *Salix*

1. *Populus L.* Cottonwood

1. Petioles strongly flattened laterally; bark of the trunk mostly smooth and white

. 2. *P. tremuloides*

1. Petioles terete or nearly so; bark of the trunk not as above, generally ashy gray . . 1. *P. angustifolia*

1. *Populus angustifolia* James. Common along streams. Saskatchewan and Alberta, south to Nebraska, New Mexico and Arizona. Big Lost River, Butte Co., 4 September 1967, 1028.

2. *Populus tremuloides* Michx. Common in sandy or gravelly soil of mountains and hillsides. Southern Labrador to Alaska, south to New Jersey, New Mexico and Arizona. Webb Springs, Butte Co., 1 July 1967, 1090.

2. *Salix L.* Willow

1. Stamens 3 to 8; leaves narrow, finely serrulate, more than three times as long as broad; filaments hairy at base 3. *S. lasiandra*

1. Stamens mostly 2 or less; other characters various 2

2. Scales of the aments early deciduous; leaves 5 to 15 times as long as wide, narrow, stigmas lobed nearly to the base 2. *S. exigua*
2. Scales of the aments persistent, mostly brown to blackish; leaves usually broader 3
3. Ovaries and capsules glabrous 4
3. Ovaries and capsules more or less densely short-hairy to sparsely hairy with age 5
4. Aments appearing before the leaves (precocious); fruits 3 to 5 mm long; leaves oblanceolate 4. *S. lasiolepis*
4. Aments coetaneous or serotimous; leaves loosely long-woolly-villous when young, less so with age, entire to toothed 1. *S. commutata*
5. Style mostly 0.7-1.7 mm long; leaves glabrous when fully expanded 5. *S. phylicifolia*
5. Style 0.5-0.8 mm long; leaves reddish-strigose beneath, sometimes glabrous 6. *S. scouleriana*

1. *Salix commutata* Bebb. Wet places at middle to high elevations, July to September. Western Wyoming to northern Utah into northern California, north through central and southeastern Idaho to southern Yukon and southern Alaska. Birch Creek, Clark Co., 25 June 1967, 1055.

2. *Salix exigua* Nutt. Moist situations, commonly along streams, Washington and Oregon to Wyoming and Colorado. Big Lost River, Butte Co., 29 July 1967, 1192. Birch Creek, Clark Co., 25 May 1967, 854B.

3. *Salix lasiandra* Benth. Stream banks, Upper Sonoran and Transition Zones. California and New Mexico, north to British Columbia and Alberta, sparingly to Alaska and the Yukon. T.2N., R.29E., Butte Co., 4 July 1967, 1123.

4. *Salix lasiolepis* Benth. Along streams at lower elevations. British Columbia to Baja California, east to northern and southwestern Idaho, Nevada, southern Utah, western Texas and adjacent Mexico. Webb Springs, Butte Co., 1 July 1967, 1084.

5. *Salix phylicifolia* L. var. *monica* (Bebb) Jeps. Diverse in habitat, usually in moist places. West central Montana and central Idaho to New Mexico, Utah, Nevada, and eastern California. North of Junction 28-22, Clark Co., 25 May 1967, 854A.

6. *Salix scouleriana* Barratt. Transition and Canadian Zones. Alaska and Yukon to California, Arizona, and New Mexico, east to Manitoba and South Dakota. Near Big Butte, Butte Co., 19 June 1950, AEC, s.n., (IDS).

SANTALACEAE. SANDALWOOD FAMILY

1. *Commandra* Nutt. False Toad-Flax

1. *Commandra umbellata* (L.) Nutt. var. *pallida* (DC.) Jones. Commonly in sandy to well drained soil, April to August. Western United States and southern Canada. R.31E., T.6N., Butte Co., 8 June 1967, 915.

SAXIFRAGACEAE. SAXIFRAGE FAMILY

1. Plants usually bulblet-bearing above or below ground level; styles or branches 3 2. *Lithophragma*
1. Plants not bearing bulblets; styles or branches usually 2 1. *Heuchera*

1. *Heuchera* L. Alumroot

1. *Heuchera parviflora* Nutt. ex T. & G. Gravelly to talus slopes, June to August. Utah and New Mexico, and Colorado, north to Wyoming, central Idaho and Nevada. Big Butte, Butte Co., 1 July 1967, 1102.

2. *Lithophragma* Nutt. Woodland Star

1. *Lithophragma tenella* Nutt. Dry sagebrush plains, May to June. Washington to southern Oregon east through central and southern Idaho to Montana and Wyoming. S.W. of East Butte, Bingham Co., 1 May 1967, 770.

SCROPHULARIACEAE. FIGWORT FAMILY

1. Anther-bearing stamens 5; corolla more or less regular 7. *Verbascum*
1. Anther-bearing stamens 2 or 4; corolla mostly irregular 3. *Veronica*
2. Anther-bearing stamens mostly 2; corolla nearly regular 4. *Linaria*
2. Anther-bearing stamens 4; corolla irregular 5
3. Corolla with a slender spur at the base 4
3. Corolla without a spur 5
4. Corolla with a fifth sterile stamen present, sometimes reduced; leaves opposite or whorled 6
4. Corolla without a fifth sterile stamen; leaves alternate or opposite 6
5. Plants annual, small, lax and weak; sterile stamen reduced and glandlike 2. *Collinsia*
5. Plants perennial, large and usually stout; sterile stamen slender and elongate 6. *Penstemon*
6. Flowers borne in heads or spikes; corolla glaucous, forming a hood or beak 7
6. Flowers axillary; corolla bilabiate, but not forming a hood or beak 5. *Mimulus*
7. Galea surpassing the lower lip; plants perennial 1. *Castilleja*
7. Galea about equal with the lower lip; plants annual 3. *Cordylanthus*

1. *Castilleja* Mutis. Indian Paintbrush

1. Bracts yellow to yellowish; palea short, rarely over $\frac{1}{2}$ the length of the corolla tube 2. *C. longispica*
1. Bracts red or purple; galea usually longer, sometimes as long or longer than the length of the corolla tube 1. *C. angustifolia*

1. *Castilleja angustifolia* (Nutt.) G. Don. Commonly in sagebrush of lower elevations, May to July. Wyoming, Idaho and eastern Oregon. Webb Springs, Butte Co., 22 May 1967, 825. R.32E., T.3N., Bingham Co., 18 May 1967, 765.

2. *Castilleja longispica* A. Nels. Sagebrush plains and lower meadows, May to July. Idaho, west to Oregon and California, east to Wyoming and Montana. Webb Springs, Butte Co., 22 May 1967, 826. Southwest of Atomic City, Butte Co., 26 May 1967, 863.

2. Collinsia Nutt. Blue-eyes Mary

1. *Collinsia parviflora* Dougl. Variable in habitat from low elevations to high in the mountains, March to July. Ontario to British Columbia, south to Michigan, Colorado to Arizona and California. Southwest of East Butte, Bingham Co., 18 May 1967, 771. T.1N., R.30E., 22 May 1967, 822.

3. Cordylanthus Nutt. Bird's-beak

1. *Cordylanthus ramosus* Nutt. ex Benth. Usually growing in sagebrush or open places, June to August. Oregon and California, east to Wyoming and Colorado. NRTS, Goodwin, 139, (NRTS).

4. Linaria Mill. Toad flax; Butter and Eggs

1. *Linaria vulgaris* Hill. Scattered, mostly in waste places, June to September. Over much of temperate North America; Eurasia. Birch Creek, Clark Co., 5 September 1967, 1211.

5. Mimulus L. Monkey Flower

1. *Mimulus nanus* H. & A. Sandy or gravelly soil of the plains, May to April. Idaho, west to Washington, Oregon and California, east and south from Montana to Nevada. R.29E., T.3N., 21 May 1967, Butte Co., 818.

6. Penstemon Mitch. Beardtongue

1. Leaves sharply toothed (sometimes entire); flowers white or whitish; plants distinctly woody at the base 2. *P. deustus*

1. Leaves mostly entire; flowers blue to bluish-white; plants not distinctly woody 2

2. Corolla large 20 to 40 mm long; palate glabrous 1. *P. cyaneus*

2. Corolla smaller, usually less than 25 mm long; palate bearded 3

3. Calyx elongate, 7 to 11 mm long; corolla 18 to 30 mm long, inflated; staminode in at least some flowers exerted 3. *P. eriantherus*

3. Calyx 7 mm long or less; corolla mostly less than 18 mm, not inflated, narrow; staminode included 4

4. Plants small less than 2 dm tall; corolla glabrous within 5. *P. pumilus*

4. Plants mostly over 2 dm tall; corolla bearded on the palate 5

5. Basal rosette well developed; calyx 2.5 to 6 mm long; corolla 10 to 17 mm long, not whitish ventrally; capsule 4 to 6 mm long 4. *P. humilis*

5. Leaves mostly cauline; calyx 5 to 9 mm long; corolla 16 to 25 mm long, whitish ventrally; capsule 5 to 8 mm long 6. *P. radicosus*

1. *Penstemon cyaneus* Pennell. Often in sagebrush and open places on the plains to middle elevations in the mountains, June to August. Idaho, east to Wyoming and Montana. Flood Control Area, Butte Co., 1 July 1967, 1099.

2. *Penstemon deustus* Dougl. Rocky, dry ground to middle elevations, May to July. Idaho, west from Washington to California, east to Montana and Wyoming, south to Utah and Nevada. T.1N., R.30E., Butte Co., 13 June 1967, 963.

3. *Penstemon eriantherus* Pursh. var. *redactus* Pennell & Keck. Mostly on dry ground in the plains and foothills, May to July. Idaho, west from British Columbia to Oregon, east to North Dakota, Nebraska and Colorado. R.29E., T.7N., 8 June 1967, 920.

4. *Penstemon humilis* Nutt. ex Gray. Frequently dry, open places on the plains and foothills to well up in the mountains, May to July. Central Idaho, west to Washington, Oregon and California, south to Utah, Nevada, Wyoming and Colorado. R.29E., T.7N., Butte Co., 10 June 1967, 932.

5. *Penstemon pumilus* Nutt. Commonly in sagebrush at lower elevations, May to July. Salmon River to the Snake River Plains. Idaho. R.31E., T.6N., Butte Co., 8 June 1967, 908.

6. *Penstemon radicosus* A. Nels. Associated with sagebrush or in open places, from the plains to middle elevations in the mountains, May to July. Southwestern Montana, to central and eastern Idaho, Wyoming, Utah, Nevada and Colorado. East Butte, Bingham Co., 24 May 1967, 841.

7. Verbascum L. Mullein

1. *Verbascum thapsus* L. A weedy plant, June to September. Over much of temperate North America; Eurasia. Junction of Highway 20-26, Butte Co., 4 September 1967, 1205.

8. Veronica L. Speedwell

1. Plants from rhizomes; leaves petiolate; corolla 5 to 10 mm wide; fruiting pedicels divaricate 1. *V. americana*

1. Plants fibrous-rooted; leaves sessile and clasping; corolla about 5 mm wide; fruiting pedicels strongly ascending 2. *V. anagallis-aquatica*

1. *Veronica americana* Schwein. Moist places at lower elevations to higher in the mountains, May to July. Over most of temperate North America. Birch Creek, Clark Co., 25 June 1967, 1056. Webb Springs, Butte Co., 1 July 1967, 1088.

2. *Veronica anagallis-aquatica* L. Along streams or other moist habitats, June to September. Over much

of the United States; Europe. Big Lost River, Butte Co., 13 July 1967, 1144.

SOLANACEAE. POTATO OR NIGHTSHADE FAMILY

1. Corolla over 2 cm long, funnellform or salverform; fruit a capsule 1. *Nicotiana*
1. Corolla less than 2 cm long, rotate to campanulate; fruit a berry 2. *Solanum*

1. *Nicotiana* L. Tobacco

1. *Nicotiana attenuata* Torr. Commonly in sandy soil, moist or dry rocky slopes and hills, June to September. Idaho, west from British Columbia to California, east to Texas. Big Lost River, Butte Co., 13 July 1967, 1151.

2. *Solanum* L. Nightshade

1. *Solanum dulcamera* L. Along streams or in thickets. May to September. Common in the United States and southern Canada; Eurasia. Birch Creek, Clark Co., 5 September 1967, 1218. Poisonous.

UMBELLIFERAE. PARSLEY FAMILY

1. Fruit bristly-hispid; leaves with well defined leaflets, not dissected 3. *Osmorhiza*
1. Fruit not bristly-hispid; leaves more or less dissected, without broad leaflets 2
2. Mature fruit with both lateral and dorsal wings, ovoid to oblong 1. *Cymopterus*
2. Mature fruit with lateral wings only, linear to obicular 2. *Lomatium*

1. *Cymopterus* Raf.

1. Plants mostly with 1 to 2 pseudoscapces; leaves forming a flat rosette 1. *C. acaulis*
1. Plants caespitose, with several leafy stems 2
2. Flowers white; calyx teeth wanting; plants acaulescent 2. *C. bipinnatus*
2. Flowers yellow; calyx teeth evident; plants caulescent 3. *C. terebinthinus*
1. *Cymopterus acaulis* (Pursh) Raf. Dry plains and valleys, April to May. Central Saskatchewan and western Minnesota to Colorado, Montana and central Idaho to Oregon. Southwest to Howe, Butte Co., 12 April 1939, Davis, s.n., (IDS).

2. *Cymopterus bipinnatus* Wats. Open rocky places, from the foothills to above timberline, May to July. Montana and Wyoming, to central Idaho, Oregon, Nevada and Utah. Near Howe, Butte Co., July 1939, O. Mays, s.n., (IDS).

3. *Cymopterus terebinthinus* (Hook) T. & G. Dry, sandy or rocky ground on the plains and foothills, April to June. Central Idaho, east to Montana, west to Oregon and Washington. R.29E., T.3N., 6 June 1967, 881. Our plants belong to the poorly de-

fined varieties *foeniculaceus* (T. & G.) Cronq. and *calcareus* (T. & G.) Cronq.

2. *Lomatium* Raf. Desert Parsely

1. Ultimate leaf segments (at least some) over 1 cm long 2
1. Ultimate leaf segments less than 1 cm long 2. *L. foeniculaceum*
2. Some of the ultimate leaf segments 3 mm wide and over 1 cm long; taproot elongate and seldom thickened 3. *L. triternatum*
2. Ultimate leaf segments less than 3 mm wide and barely over 1 cm long; taproot very large and woody 1. *L. dissectum*
1. *Lomatium dissectum* (Nutt.) Math. & Const. var. *multifidum* (Nutt.) Math. & Const. Rocky plains and slopes, April to June. British Columbia and Alberta to Wyoming, west through central Idaho to Oregon and Nevada. Webb Springs, Butte Co., 24 May 1967, 842.

2. *Lomatium foeniculaceum* (Nutt.) Coult. & Rose var. *macdougalii* (Coult. & Rose) Cronq. Valleys and plains to higher in the mountains, April to August. Central and southern Idaho, west to Oregon to Arizona and Nevada, east to Montana to the southern Great Plains. T.4N., 4.28E., Butte Co., 21 May 1967, 810.

3. *Lomatium triternatum* (Pursh) Coult. & Rose From the dry plains to higher, moist habitats, May to July. Alberta and British Columbia to Colorado, Utah and California. T.4N., R.28E., Butte Co., 21 May 1967, 809.

3. *Osmorhiza* Raf. Sweet Cicely

1. *Osmorhiza chilensis* Hook & Arm. Mainly in moist wooded areas, April to June. Idaho, north and west from Alaska to California, east from Alberta, South Dakota, Colorado to Arizona; Chile and Argentina. Webb Springs, Butte Co., 1 July 1967, 1083.

URTICACEAE. NETTLE FAMILY

1. *Urtica* L. Nettle

1. *Urtica dioica* L. ssp. *gracilis* var. *holosericea* (Nutt.) Hitchc. Sagebrush plains to mountain slopes, May to September. Widespread. Big Butte, Butte Co., 27 June 1950, AEC, 137, (IDS).

VERBENACEAE. VERBENA FAMILY

1. *Verbena* L. Verbena

1. *Verbena bracteata* Lag. & Rodr. A weedy plant along roads, waterways, and disturbed areas, May to September. Throughout most of temperate North America. Big Lost River, Butte Co., 13 July 1967, 1143.

VIOLACEAE. VIOLET FAMILY

1. *Viola* L. Violet

1. *Viola nuttallii* Pursh Commonly in sagebrush, from the plains to the mountains, April to July. British Columbia to California, east to the central United States. Webb Springs, Butte Co., 22 May 1967, 828.

CLASS ANGIOSPERMAE

SUBCLASS MONOCOTYLEDONEAE

Key to the Families

1. Perianth lacking or inconspicuous, of bristles or scales, not petallike (see also Juncaginaceae and Juncaceae) 2
1. Perianth commonly of 2 series, the inner usually petaloid (except in Juncaceae and Juncaginaceae) 4
2. Flowers sessile in the axils of chaffy, imbricate bracts; plants with jointed stems and sheathing leaves, grasslike; fruit 1-seeded. . . .3
2. Flowers not sessile in the axils of chaffy bracts; fruit of 3 to 6 carpels JUNCAGINACEAE, p. 42
3. Stems round or flat and mostly hollow; leaves 2-ranked; anthers attached at the middle GRAMINEAE, p. 39
3. Stems mostly triangular and solid; leaves 3-ranked; anthers attached at the base CYPERACEAE, p. 39
4. Perianth segments greenish or brownish, not showy; plants somewhat grasslike 5
4. Inner perianth divisions showy and petallike; plants not grasslike 6
5. Carpels 3 to 6, separating at maturity; flowers in racemes or spikes JUNCAGINACEAE, p. 42
5. Carpels 1 to 3, united; inflorescence paniculate or corymbose JUNCACEAE, p. 42
6. Pistils several to many in a head or ring, each ovary with 1-carpel ALISMACEAE, p. 39
6. Flowers with a single pistil, of several united carpels 7
7. Stamens 3 or fewer; ovary inferior 8
7. Stamens commonly 6; ovary superior LILIACEAE, p. 42
8. Perianth irregular; stamens 1 or 2 ORCHIDACEAE, p. 43
8. Perianth usually regular; stamens commonly 3 IRIDACEAE, p. 42

ALISMACEAE. WATER PLANTAIN FAMILY

1. *Alisma* L. Waterplantain

1. *Alisma plantago-aquatica* L. In water and wet places, June to September. Found over most of the United States and Canada. Sinks, Butte Co., 5 September 1967, 1222.

CYPERACEAE. SEDGE FAMILY

1. Achene enclosed by an inner scale (perigynium); flowers imperfect; perianth lacking 1. *Carex*
1. Achenes subtended by 1 outer flat scale, not enclosing the achene; some flowers of each spikelet perfect; perianth of 1 to 12 bristles 2. *Eleocharis*

1. *Carex* (Rupp.) L. Sedge

1. *Carex douglasii* Boott. Open more or less dry ground, April to August. Manitoba to British Columbia, south to California and New Mexico. Shell Road, Butte Co., 25 May 1967, 848. There are probably more species in this genus and in the family which occur on the site particularly in the sinks area. This area, during the period of this work, received an unusual amount of runoff and was quite inaccessible.

2. *Eleocharis* R. Br. Spikerush

1. *Eleocharis palustris* (L.) R. & S. Moist or wet ground, May to August. Alaska and British Columbia, south to California and Mexico. Five miles S.E. of Big Butte, 24 June 1950, AEC, 172, (IDS).

GRAMINEAE. GRASS FAMILY

1. Spikelets with one perfect terminal floret and a sterile or staminate floret below; articulating below the spikelet 5. *Echinochloa*
1. Spikelets 1 to many flowered, reduced florets, when present, above the perfect florets; articulation above the glumes 2
2. Spikelets sessile or subsessile in spikes or spike-like racemes 3
2. Spikelets pedicellate in open or contracted panicles 6
3. Spikelets solitary at each node of the rachis 1. *Agropyron*
3. Spikelets more than one at each node of the rachis (*Elymus* with part of the spike with solitary spikelets) 4
4. Spikelets 3 at each node of the rachis, usually 1-flowered, the lateral ones pedicelled, usually reduced to awns 8. *Hordeum*
4. Spikelets 2 at each node of the rachis, 2 to 6-flowered 5
5. Rachis readily disarticulating, glumes subulate and produced into long divergent awns 14. *Sitanion*
5. Rachis continuous, glumes broad or narrow, acute to aristate, entire 6. *Elymus*
6. Spikelets 1-flowered 7
6. Spikelets 2 to many flowered 11
7. Fruit indurate, terete, awned; callus well developed, bearded 8
7. Fruit thin or firm; callus not well developed, . .10
8. Awn trifid, the lateral ones sometimes short 3. *Aristida*

8. Awn simple 9
 9. Awn not twisted (early deciduous), usually less than 3 to 4 times as long as the fruit; callus mostly obtuse 11. *Oryzopsis*
 9. Awn twisted, persistent, and bent, more than 4 times longer than the fruit; callus sharp pointed 16. *Stipa*
 10. Glumes longer than the lemma; palea small or wanting 2. *Agrostis*
 10. Glumes not longer than the lemma, mostly shorter; palea well developed ... 15. *Sporobolus*
 11. Glumes at least as long as the lowest floret; lemmas awnless or awned from the back 9. *Koeleria*
 11. Glumes shorter than the first floret, lemmas awnless or awned from the tip or a bifid apex ... 12
 12. Plants large, culms 2 m or more tall; panicles large, plumelike 12. *Phragmites*
 12. Plants smaller, culms less than 1.5 m tall 13
 13. Lemmas awnless, mostly rounded on the back 14
 13. Lemmas mucronate or awned, keeled at least toward the summit 15
 14. Glumes papery; upper florets reduced 10. *Melica*
 14. Glumes not papery; upper florets similar to the lower ones; blades with boat shaped tips 13. *Poa*
 15. Lemmas awned from between the teeth of the minutely bifid apex 4. *Bromus*
 15. Lemmas awnless; plants dioecious; stigmas subplumose 7. *Hesperochloa*
1. *Agropyron* Gaertn. Wheatgrass
 1. Plants with creeping rhizomes 2
 1. Plants without creeping rhizomes 5
 2. Lemmas awned, the awn divergent at maturity; lemmas pubescent 1. *A. albicans*
 2. Lemmas awnless or with a short straight awn ...3
 3. Glumes rigid, tapering into a short awn 5. *A. smithii*
 3. Glumes not rigid, acute or abruptly awn pointed 4
 4. Joints of the rachilla villous; lemmas villous 2. *A. dasystachyum*
 4. Joints of the rachilla glabrous or scaberulous 4. *A. riparium*
 5. Spikelets much compressed, crowded on the rachis 3. *A. desertorum*
 5. Spikelets not much compressed, not crowded on the rachis 6
 6. Spikelets awnless or nearly so; lemmas glabrous . 8. *A. trachycaulum*
 6. Spikelets awned 7
 7. Awn straight or nearly so, blades 3 to 8 mm wide; glumes 4 to 7-nerved 7. *A. subsecundum*
 7. Awn divergent when dry; blades 1 to 2 mm wide; glumes about 4-nerved 6. *A. spicatum*
 1. *Agropyron albicans* Scribn. & Smith. Plains and dry hills. South Dakota to Alberta and Idaho, Colorado and Utah. R.30E., T.5N., Butte Co., 13 June 1967, 986.
 2. *Agropyron dasystachyum* (Hook.) Scribn. Plains and sandy shores, May to July. Michigan to British Columbia, south to Illinois, Nebraska, Colorado, Nevada and Oregon. By cave near EBR. II Reactor, Bingham Co., 30 June 1967, 1061. T.6N., R.32E., Jefferson Co., 28 July 1967, 1178. T.4N., R.31E., Butte Co., June 1965, Harniss, (UTC).
 3. *Agropyron desertorum* (Fish.) Schult. Russia; widespread in the western United States, June to August. R.30E., T.5N., Butte Co., 13 June 1967, 985.
 4. *Agropyron riparium* Scribn. & Smith Dry or moist meadows and hills, May to July. Western United States and southern Canada. EBR. I, Butte Co., 4 July 1967, 1124.
 5. *Agropyron smithii* Rydb. Moist, usually alkaline soil, June to August. Widespread in east and western North America and southern Canada. R.30E., T.5N., Butte Co., 13 June 1967, 987.
 6. *Agropyron spicatum* (Pursh) Scribn. & Smith Plains, canyons, and slopes, June to August. Alaska, south to California, east to New Mexico, South Dakota and Michigan. Webb Springs, Butte Co., 13 June 1967, 974.
 7. *Agropyron subsecundum* (Link) Hitchc. var. *andinum* (Scribn. & Smith) Hitchc. Mountain meadows and slopes. Montana to Washington, south to Colorado and Nevada. East Butte, Bingham Co., 22 June 1967, 1011.
 8. *Agropyron trachycaulum* Malte. Alaska to Labrador, south to California, Mexico, West Virginia and Missouri. T.2N., R.29E., Butte Co., 4 July 1967, 1124. T.6N., R.32E., Jefferson Co., 28 July 1967, 1179.
2. *Agrostis* L. Bentgrass
 1. *Agrostis alba* L. Cultivated extensively and escaping, June to September. Mostly in the cooler parts of the United States, Eurasia. Big Lost River, Butte Co., 29 July 1967, 1191.
 3. *Aristida* L. Three-awn
 1. *Aristida fendleriana* Steud. Plains and hills, June to July. North Dakota to Montana, south to Texas, Nebraska and California; Mexico. Tractor Flat, Jefferson Co., 22 July 1967, 1197.
 4. *Bromus* L. Brome grass
 1. Plants perennial 1. *B. inermis*
 1. Plants annual 2
 2. Lemmas narrow, with a sharp callus, gradually acuminate, bifid; awns usually 1.5 cm long or more 2. *B. tectorum*

2. Lemmas broad, rounded above, not acuminate; sheaths glabrous 3. *B. secalinus*

1. *Bromus inermis* Leyss. Cultivated, escaping, June to August. Europe; northern half of the United States. R.30E., T.5N., Butte Co., 13 June 1967, 984.

2. *Bromus secalinus* L. A weed, throughout most of the United States, June to July. Birch Creek, Clark Co., 25 June 1967, 1054.

3. *Bromus tectorum* L. Along roadsides and waste places, April to June. Sporadic in the United States as far as South Carolina and Texas. R.28E., T.4N., Butte Co., 21 May 1967, 817.

5. *Echinochloa* Beauv.

1. *Echinochloa crusgalli* (L.) Beauv. Moist places, June to October. Widespread. Sec. 33, T.5N., R.30E., Butte Co., 26 July 1956, McBride, 74, (NRTS).

6. *Elymus* L. Wildrye

1. Plants with slender, creeping rhizomes 3. *E. flavescens*

1. Rhizomes wanting or short and stout in *E. cinereus*; plants tufted 2

2. Spike 1 to 2 cm thick; spikelets usually 2 to 5 at a node; culms many 2. *E. cinereus*

2. Spike more slender; some or most of the spikelets solitary at the nodes; culms few 1. *E. ambiguus*

1. *Elymus ambiguus* Vasey & Scribn. Open slopes, May to July. Montana, Colorado, Idaho and Utah. R.30E., T.6N., Butte Co., 11 June 1967, 946.

2. *Elymus cinereus* Scribn. & Merr. Moist river banks or dry slopes and plains, June to July. Minnesota to British Columbia, south to California and Colorado. Flood Control Area, Butte Co., 1 July 1967, 1110.

3. *Elymus flavescens* Scribn. & Smith Sand dunes, June to July. Eastern Washington and Oregon, Idaho, South Dakota. R.31E., T.6N., Butte Co., 28 July 1967, 1180.

7. *Hesperochloa* (Piper) Rydb.

1. *Hesperochloa kingii* (S. Wats.) Rydb. Mountains and hills, June to August. Oregon to California, east to Montana, Nebraska and Colorado. Webb Springs, Butte Co., 13 June 1967, 971.

8. *Hordeum* L. Barley

1. *Hordeum jubatum* L. Moist soil, especially in saline areas, June to August. Newfoundland to Alaska, south to Texas. California, and Mexico. Junction 88-22, Butte Co., 13 June 1967, 983.

9. *Koeleria* Pers. Junegrass

1. *Koeleria cristata* (L.) Pers. Prairie, open woods, and sandy soil, May to July. Ontario to British Columbia, south to Delaware, Louisiana, Mexico and California. East Butte, Bingham Co., 22 June 1967, 1015. Webb Springs, Butte Co., 15 July 1967, 1155.

10. *Melica* L. Meliograss; Oniongrass

1. *Melica bulbosa* Geyer. Woods and hills, May to July. British Columbia, south to California, Colorado and Texas. Big Butte, Butte Co., 13 June 1967, 982.

11. *Oryzopsis* Michx. Ricegrass

1. *Oryzopsis hymenoides* (R. & S.) Richer. Deserts and plains, May to June. Manitoba to British Columbia, south to California, Texas and New Mexico. Two miles west of Big Lost River Bridge, Butte Co., 6 June 1967, 887.

12. *Phragmites* Trin. Common reed

1. *Phragmites communis* Trin. Marshes, banks, and other moist places, August to September. Cosmopolitan. Should be looked for on the Big Lost River and in the Sinks area.

13. *Poa* L. Bluegrass

1. Spikelets distinctly compressed, the glumes and lemmas keeled 2

1. Spikelets little compressed, narrow, much longer than wide; lemmas convex on the back 3

2. Creeping rhizomes present; lemmas webbed at the base 5. *P. pratense*

2. Creeping rhizomes wanting; lemmas not webbed at the base 2. *P. fendleriana*

3. Lemmas crisp—puberulent on the back toward the base 4

3. Lemmas glabrous or minutely scabrous, but not crisp-puberulent 5

4. Culms slender mostly less than 30 cm tall; numerous short innovations at base; blades usually folded 6. *P. secunda*

4. Culms stouter, usually more than 30 cm tall; innovations usually not numerous . . . 1. *P. canbyi*

5. Sheaths scaberulous; ligules long, decurrent 4. *P. nevadensis*

5. Sheaths glabrous; blades involute 3. *P. juncifolia*

1. *Poa canbyi* (Scribn.) Piper Dry soil. Yukon to Michigan, south to Nebraska, Arizona and California. T.2N., R.29E., Butte Co., 4 July 1967, 1125. Eight miles east of Howe, Butte Co., 27 June 1941, Hull 265. (IDS).

2. *Poa fendleriana* (Steud.) Vasey Rocky slopes and mesas, May to August. British Columbia to Manitoba, south to South Dakota, Nebraska, and Idaho to Texas and California; New Mexico. R.29E., T.3N., Butte Co., 23 May 1967, 833.

3. *Poa juncifolia* Scribn. Saline soil, May to July. British Columbia to Montana, south to California and Colorado. Desert, Butte Co., June 1950, AEC, 41, (IDS).

4. *Poa nevadensis* Vasey ex Scribn. Moist places, June to July. Montana to eastern Washington and the Yukon, south to Colorado, Arizona, and California; Maine. East Butte, Bingham Co., 3 July 1950, AEC

Project, 170 (IDS). T.3N., R.29E., Butte Co., 7 June 1967, 892.

5. *Poa pratense* L. Open woods, meadows and plains, May to October. Widespread throughout the United States and northward; Europe. R.29E., T.3N., 21 May 1967, 833.

6. *Poa secunda* Presl. Plains, dry woods and rocky slopes. North Dakota to the Yukon, south to California, New Mexico, Nebraska; Chile. T.2N., R.29E., Butte Co., 4 July 1967, 1125.

14. *Sitanion* Raf. Squirreltail

1. *Sitanion hystrix* (Nutt.) J. G. Smith. Dry hills, plains and woods, May to July. South Dakota to British Columbia, south to California, Texas and Missouri. T.6N., R.31E., Butte Co., June 1957, McBride, s.n., (UTC).

15. *Sporobolus* R. Br. Dropseed

1. *Sporobolus cryptandrus* (Torr.) Gray. Sandy open ground, June to July. Alberta to Ontario, south to Washington, North Carolina, Indiana, Louisiana, southern California, and New Mexico; Maine. R.31E., T.4N., Butte Co., 4 July 1967, 1120.

16. *Stipa* L. Needlegrass

1. Awn plumose below, the hairs ascending or spreading 2

1. Awn scabrous or nearly glabrous, rarely appressed-hispid, not plumose 3

2. Ligules 3 to 6 mm long, hyaline 4. *S. thurberiana*

2. Ligules minute, mostly hairy. . . 3. *S. occidentalis*

3. Lemmas mostly more than 1 cm long, glabrous or sparsely pubescent above the callus 2. *S. comata*

3. Lemmas 7 mm long or less; distinctly pubescent on the upper part at least 1. *S. columbiana*

1. *Stipa columbiana* Macoun. Dry plains and woods, May to August. South Dakota to Yukon Territory, south to California and Texas. Webb Springs, Butte Co., 1 July 1967, 1073.

2. *Stipa comata* Trin. & Rupr. Plains and hills, May to July. Indiana to Yukon Territory, south to California and Texas. R.28E., T.4N., Butte Co., 21 May 1967, 816.

3. *Stipa occidentalis* Thurb. Plains, hills, and woods, May to August. Wyoming to Washington, Arizona, and California. East Butte, Bingham Co., 22 June 1967, 1010 Webb Springs, Butte Co., 1 July 1967, 1073.

4. *Stipa thurberiana* Piper. Rocky slopes and plains, May to June. Idaho to Washington and California. South of Middle Butte, Bingham Co., 22 June 1967, 1028.

IRIDACEAE. IRIS FAMILY

1. *Iris* L.

1. *Iris missouriensis* Nutt. Moist meadows, marshes and along streams. New Mexico and California, north to British Columbia and North Dakota, 5,000 to 10,000 feet. May to July. Birch Creek, Clark Co., 25 June 1967, 1040.

JUNCACEAE. RUSH FAMILY

1. *Juncus* L. Rush

1. *Juncus balticus* Willd. Moist places, June to August. Montana to Alaska, south to Kansas, New Mexico and California. Birch Creek, Clark Co., 25 June 1967, 1038.

JUNCAGINACEAE. ARROWGRASS FAMILY

1. *Triglochin* L. Arrowgrass

1. *Triglochin palustris* L. Greenland to Alaska, south to most of the northeastern United States and scattered in the western states, June to August. Birch Creek, Clark Co., 25 June 1967, 1039.

LILIACEAE. LILY FAMILY

1. Perianth segments all alike or nearly so 2

1. Perianth segments unlike, 3 outer small and sepals, 3 inner large and petaloid 2. *Calochortus*

2. Flowers borne on scapose peduncles, in umbels; when fresh, emitting an onionlike odor 1. *Allium*

2. Flowers not in umbels, on scapose peduncles; onion odor not present 3

3. Plants from bulbs or corms; fruit a capsule; leaves linear-lanceolate 4

3. Plants from rootstocks; fruit a berry, leaves lanceolate 4. *Smilacina*

4. Flowers small, usually 1 cm long or less; styles 3, distinct; flowers whitish 5. *Zygadenus*

4. Flowers usually over 1 cm long; style 1, entire or divided; flowers purple, brown, or yellow 3. *Fritillaria*

1. *Allium* L. Onion

1. Outer bulb coats of coarse anastomosing fibers; ovary crested with 6 low knobs 2

1. Outer bulb coats without fibers, never fibrous-reticulate; ovary inconspicuously 3 crested 1. *A. acuminatum*

2. Leaves commonly 2 per scape; tips of the inner perianth segments spreading; flowers usually white 3. *A. textile*

2. Leaves usually 3 or more per scape; tips of the inner perianth segments erect; flowers commonly pink 2. *A. geyeri*

1. *Allium acuminatum* Hook. Dry plains and hills, May to July. British Columbia south to Wyoming, Colorado and California. South of Middle Butte,

Bingham Co., 22 June 1967, 1052. Arco Desert, Butte Co., June 1950, AEC, 67, (IDS).

2. *Allium geyeri* S. Wats. Plains, meadows and slopes, May to June. Alberta, south to Texas, Arizona and Washington. South of Middle Butte, Bingham Co., 22 June 1967, 1025. R.29E., T.7N., Butte Co., 10 June 1967, 935.

3. *Allium textile* Nels. & Macbr. Plains and dry hills, May to June. Saskatchewan to Alberta, south to New Mexico and Arizona. R.28E., T.4N., Butte Co., 20 May 1967, 794.

2. *Calochortus* Pursh. Sego lily
1. Sepals usually exceeding the petals; anthers linear 2. *C. macrocarpus*
1. Sepals shorter than the petals; anthers oblong to lanceolate 1. *C. bruneauensis*
1. *Calochortus bruneauensis* Nels. & Macbr. Dry soil, June to July. Nevada and adjacent Oregon in the southeastern part, southwestern Idaho and south-western Montana. R.34E., T.5N., Jefferson Co., 20 June 1967, 1006.

2. *Calochortus macrocarpus* Dougl. Montana to British Columbia, south to Nevada and northeastern California, May to July. East Butte, Bingham Co., 23 July 1967, 1175.

3. *Fritillaria* L.
1. Flowers dull purple, mottled with greenish-yellow; capsule sharply angled 1. *F. atropurpurea*
1. Flowers bright yellow-orange, when young; capsule obtusely lobed 2. *F. pudica*
1. *Fritillaria atropurpurea* Nutt. Dry plains and slopes, May to June. North Dakota across central and southern Idaho, to Oregon, south to California and New Mexico, April to June. Six miles S.W. of Atomic City, Butte Co., 22 May 1967, 821. Webb Springs, Butte Co., 26 May 1967, 876.

2. *Fritillaria pudica* (Pursh) Spreng. Plains and hillsides, March to June. Montana to British Columbia, south to Utah and California, April to June. Webb Spring, Butte Co., 21 April 1967, 751.

4. *Smilacina* Desf. False Solomon's seal
1. *Smilacina stellata* (L.) Desf. Moist, usually shaded ground, May to June. Throughout most of temperate North America; Europe, May to June. Webb Springs, Butte Co., 15 July 1967, 1159. Big Lost River, Butte Co., 13 July 1967, 1150.

5. *Zygadenus* Michx. Death camas
1. Flowers mostly paniculate; perianth-parts acute or acuminate; plants of dry areas in the foothills 1. *Z. paniculatus*
1. Flowers commonly racemose; perianth-parts obtuse or rounded at apex; plants of moist areas in the mountains 2. *Z. venenosus*

1. *Zigadenus paniculatus* (Nutt.) Wats. Montana to Washington, south to California and New Mexico, 5,500 to 8,000 feet. May to June. R.28E., T.4N., Butte Co., 21 May 1967, 811.
2. *Zigadenus venenosus* S. Wats. Montana to British Columbia, south to Utah and California, June to July. Big Butte, Butte Co., 1 July 1967, 1103.

ORCHIDACEAE. ORCHID FAMILY

1. *Corallorhiza* (Hall.) Chat. Coral root
1. *Corallorhiza maculata* Raf. Commonly in shaded woods, on rich humus soil. Alaska to Nova Scotia, south to Florida, New Mexico and California, at 6,000 to 9,000 feet. June to July. Webb Springs, Butte Co., 1 July 1967, 1062.

CLASS GYMNOSPERMAE

Key to the Families

1. Leaves scalelike, opposite or in whorls, imbricate; cones berrylike, the scales becoming fleshy at maturity 5. CUPRESSACEAE, p. 43
1. Leaves in fascicles or solitary, needle-shaped or narrowly linear; cones elongate (more or less), dry and woody at maturity 4. PINACEAE, p. 43

CUPRESSACEAE. CYPRESS FAMILY

1. *Juniperus* L. Juniper
1. Fruit reddish-brown or bluish; seeds 1 to 2; branchlets not flattened; leaves obtuse to acute 1. *J. osteosperma*
1. Fruit bright blue; seeds 1 to 3; branchlets flattened; leaves acute to acuminate 2. *J. scopulorum*
1. *Juniperus osteosperma* (Torr.) Little. Dry plains and foothills. Southwestern Wyoming, southwestern Idaho, western Colorado, Utah, and western New Mexico to northern Arizona and the southeastern part of California. R.28E., T.4N., Butte Co., 21 May 1967, 815.
2. *Juniperus scopulorum* Sarg. Commonly on rocky dry ridges at altitudes of 5,000 to 6,000 feet, May to June. Alberta and British Columbia, south to Arizona and Nevada. Webb Springs, Butte Co., 1 July 1967, 1068.

PINACEAE. PINE FAMILY

1. Leaves in clusters of 2 to 5, sheathed at the base, at least when young; cone scales very thick and woody 1. *Pinus*

- 1. Leaves single on the twigs, not sheathed at the base; cone scales not thick and woody 2. *Pseudotsuga*
 - 1. *Pinus* L. Pine
 - 1. Leaves 2 in a fascicle, each with 2 fibro-vascular bundles; cones 3 to 5 cm long 1. *P. contorta*
 - 1. Leaves usually 5 in a fascicle, each with 1 fibro-vascular bundle; cones 1 to 2.5 dm long 2. *P. monticola*
 - 1. *Pinus contorta* Dougl. var. *murrayana* Engel.
- Hills and mountains, commonly in dry situations, April to June. Saskatchewan to Alaska, south to California and Colorado. Big Butte, Butte Co., 7 September 1967, 1227.
2. *Pinus monticola* Dougl. Moist areas at middle altitudes in the mountains, May to June. California, north to Idaho, western Montana and British Columbia. Big Butte, Butte Co., 7 September 1967, 1228.

- 2. *Pseudotsuga* Carr. Douglas fir
 - 1. *Pseudotsuga menziesii* (Mirb.) Franco. Hills and mountains, commonly on deep soils of northern slopes, April to May. Alberta to British Columbia, south to California, Arizona and Western Texas. Webb Springs, Butte Co., 1 July 1967, 1079.

DIVISION PTERIDOPHYTA

Key to the Families

- 1. Plants with broad leaves, usually exceeding 2 cm in length; leaves petioled 2

- 1. Plants with leaves reduced to scales, sheathing the internodes at the joints; leaves sessile EUISETACEAE, p. 44
- 2. Sporangia borne in hard sporocarps; leaves palmately 4-foliate; plants rooting in mud MARSILEACEA, p. 44
- 2. Sporangia borne on the veins of the pinules, leaves bi- or tri-pinnate; plants commonly in crevices of cliffs and ledges POLYPODIACEAE, p. 44

- EUISETACEAE. HORSETAIL FAMILY
- 1. *Equisetum arvense* L. In damp soil, along streams, woods and in sterile soil of roadsides. Newfoundland to Alaska, south throughout most of the United States; Greenland; Eurasia. Birch Creek, Butte Co., 25 June 1967, 1042.

- MARSILEACEAE. PEPPERWORT FAMILY
- 1. *Marsilea vestita* Hook. & Grey. Edges of ponds, ditches and rivers. Saskatchewan, British Columbia, south to California, Texas, Arkansas and South Dakota. Sinks, Butte Co., 5 September 1967, 1223.

- POLYPODIACEAE. FERN FAMILY
- 1. *Woodsia oregana* Eaton. Common in moist or dry shaded cliffs, on talus slopes and under rocks. Quebec to British Columbia, south to California, Arizona, New Mexico and Oklahoma. Webb Springs, Butte Co., 1 July 1967, 1076.

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**MITES AND LICE OF THE
NATIONAL REACTOR TESTING STATION**

by

Dorald M. Allred



BIOLOGICAL SERIES—VOLUME XII, NUMBER 1

OCTOBER 1970

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MITES AND LICE OF THE NATIONAL REACTOR TESTING STATION¹

Dorald M. Allred*

INTRODUCTION

This is the fourth in a series of reports on arthropods of the National Reactor Testing Station in Idaho (Allred, 1968 a & b, 1969). A fifth paper by Atwood (1970) deals with the plants of the sites where the arthropods were studied. The initial publication of the series (Allred, 1968a) discusses the location and physical characteristics of the NRTS, the study areas and procedures, and lists the kinds of vertebrates examined. The reader is referred to that report for details not included herein.

The National Reactor Testing Station is situated approximately 30 miles west of Idaho Falls in southeastern Idaho. The central and southern parts are typified by basalt flows which are exposed in some areas. The northern section is primarily lake and eolian deposits, and exposed basalt flows are less evident. Annual precipitation averages less than 10 inches, and the vegetation is characteristic of the cool, northern desert, shrub-type biome. Twelve principal study sites established on the basis of their predominant vegetation were studied periodically: (1) *Chrysothamnus-Artemisia*-grasses; (2) *Artemisia-Chrysothamnus*-grasses; (3) *Elymus*; (4) *Oryzopsis-*

Stipa; (5) *Juniperus*; (6) *Chrysothamnus-Tetradymia-Artemisia*; (7) *Chrysothamnus-Artemisia-Eurotia*; (8) *Artemisia-Atriplex*; (9) *Chenopodium-Eurotia*; (10) *Artemisia-Opuntia*; (11) *Chrysothamnus-grasses-Tetradymia*; (12) *Juniperus-Chrysothamnus-Eurotia-Artemisia*. Twenty-eight other sites similar to the major ones but with minor variations of plant associations occupying smaller geographic areas were studied less frequently.

Most of the mammals were captured with live-catch or break-back traps. Rabbits, carnivores, and birds were shot, and reptiles were captured by hand or in can pit-traps. Ectoparasites were retrieved from their hosts by the cooling and warming method described by Allred (1968a).

Financial support for these studies was provided by U.S. Atomic Energy Commission Contract AT(11-1)-1559 with Brigham Young University. Logistics (in part) were provided through the AEC Operations Office at Idaho Falls, Idaho. The chigger mites and many of the mesostigmatids were identified by Mr. Morris Goates, and the lice by Dr. W. L. Jellison.

PARASITE-HOST ASSOCIATIONS

Entries in the listings below may be interpreted by using the first two lines of the listing of mite-host associations as an example (each specific entry is indicated in boldface type):

Androlaelaps leviculus (Mar-Aug) 13 dny 1 ♂ 17 ♀:
Androlaelaps leviculus = the species of parasite collected.
(Mar-Aug) = the inclusive period of time when the parasites were found.
13 dny 1 ♂ 17 ♀ = the total number of parasites of each developmental stage and sex that were collected (la = larva, pny = protonymph, dny = deuto-

nymph, im = immature, ♂ = adult male, ♀ = adult female).

Dipodomys ordii 2 (808) 1.5 - ♀: Jun Jul:

Dipodomys ordii = a specific host on which parasites of the species listed above it were found.

2 = number of hosts infested with parasites of that particular species.

(808) = total number of hosts examined.

1.5 = the parasite-host index (total number of parasites of that

¹BYU-AEC Report No. C00-1559-5.

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species found on that particular host, divided by the number of hosts of the species infested with those parasites).

♀ = the specific stage of development and/or sex of parasite found on that host.

Jun Jul = the specific months when these parasites were found on that host.

Asterisks preceding the names of the hosts indicate that of all of those listed, they are the ones most commonly infested. Except where indicated otherwise, the hosts are mammals.

Mite-Host Associations

Androlaelaps leviculus (Mar-Aug) 13 dny 1 ♂ 17 ♀
Dipodomys ordii 2 (808) 1.5 - ♀: Jun Jul
Eutamias minimus 1 (398) 1.0 - ♀: Aug
 * *Onychomys leucogaster* 2 (63) - 4.5 - dny ♀: Mar Aug
 * *Peromyscus maniculatus* 7 (1866) 2.6 - dny ♂ ♀: Mar June-Aug

Androlaelaps sp. (Jul-Sep) 3 dny 1 ♂ 7 ♀
Dipodomys ordii 3 (808) 1.0 - ♀: Jul-Aug
Onychomys leucogaster 1 (63) 4.0 - dny ♀: Aug
Perognathus parvus 1 (434) 1.0 - ♂: Aug
Peromyscus maniculatus 2 (1866) 1.5 - ♀: Aug Sep

Bernia marita (Aug-Nov) 2 la
Eremophila alpestris (bird) 1 (84) 1.0: Nov
Peromyscus maniculatus 1 (1866) 1.0: Aug

Brevisterna sp. (Aug) 2 dny
Neotoma cinerea 1 (14) 2.0

Chatia ochotona (Aug-Oct) 21 la
Neotoma cinerea 1 (14) 7.0: Aug
Plecotus townsendii 1 (78) 14.0: Oct

Dermanyssus gallinae (Feb-Jun) 1 ♂ 14 ♀
Asyndesmus lewis (bird) 1 (2) 1.0 - ♀: May
Dendrocopos villosus (bird) 1 (1) 4.0 - ♀: Jun
 * *Eremophila alpestris* (bird) 5 (84) 1.6 - ♂ ♀: Feb Apr
Turdus migratorius (bird) 1 (11) 1.0 - ♀: Jun

Dermanyssus sp. (Apr-Jun) 2 pny 2 ♀ 1 ?
Eremophila alpestris (bird) 3 (84) 1.0 - pny ♀: Apr
Piranga ludoviciana (bird) 1 (16) 1.0 - ? : Jun
Dipodomys ordii 1 (808) 1.0 - ♀: Apr

Eubrachyla elaps circularis (Mar-Jun) 4 ♀
Peromyscus maniculatus 3 (1866) 1.3: Mar Jun

Eubrachyla elaps crowei (Mar-Oct) 202 ♀
Dipodomys ordii 2 (808) .5: Sep
 * *Onychomys leucogaster* 22 (63) 8.8: Mar Jun-Aug Oct
Peromyscus maniculatus 5 (1866) 1.6: Mar Aug Oct

Eubrachyla elaps debilis (Jan-Dec) 1 pny 12 dny 1 ♂ 998 ♀
Crotalus viridis (snake) 1 (95) 1.0 - ♀: Jun
Centrocercus urophasianus (bird) 1 (18) 1.0 - ♀: Feb
Dipodomys ordii 1 (808) 5.0 - ♀: Mar Jul Aug
Onychomys leucogaster 3 (63) 5.3 - ♀: Mar
Perognathus parvus 5 (474) 1.2 - ♀: May Jun Sep
 * *Peromyscus maniculatus* 222 (1866) 4.6 - pny dny ♂ ♀: Jan-Sep Nov Dec

Eubrachyla elaps sp. (Feb-Nov) 1 pny 10 dny
Dipodomys ordii 1 (808) 1.0 - dny: Apr
Peromyscus maniculatus 1 (1866) 9.0 - dny: Feb May Jun Nov ? host - pny: Jul

Euschoengastia cordiremus (Jul-Oct) 19 la
Dipodomys ordii 1 (808) 7.0: Jul Aug
Peromyscus maniculatus 2 (1866) 6.0: Oct

Euschoengastia criceticola (Oct) 1 la
Peromyscus maniculatus 1 (1866) 1.0

Euschoengastia decipiens (Mar-Dec) 488 la
Zonotrichia leucophrys (bird) 1 (33) 3.0: Sep
 * *Dipodomys ordii* 13 (808) 7.0: Mar-May Jul Aug Oct
Eutamias minimus 4 (398) 2.8: Oct
 * *Lepus californicus* 2 (125) 11.0: Dec
Neotoma cinerea 1 (14) 3.0: Sep
 * *Perognathus parvus* 12 (474) 13.6: May Aug-Oct
 * *Peromyscus maniculatus* 14 (1866) 5.9: Apr May Jul-Nov
Sylvilagus idahoensis 1 (13) 56.0: Nov
 * *Sylvilagus nuttallii* 3 (28) 14.0: Oct-Dec
Thomomys talpoides 1 (8) 15.0: Sep

Euschoengastia fasolla (Oct) 8 la
Eutamias minimus 2 (398) 4.0

Euschoengastia lancei (Jul) 8 la
Peromyscus maniculatus 1 (1866) 8.0

Euschoengastia luteodema (Dec) 5 la
Lepus californicus 1 (125) 5.0

- Euschoengastia oregonensis* (Jul) 11 1a
Salpinctes obsoletus (bird) 1 (17) 11.0
- Euschoengastia pomerantzi* (Oct) 1 1a
Eutamias minimus 1 (398) 1.0
- Euschoengastia radfordi* (Apr-Dec) 80 1a
 * *Amphispiza belli* (bird) 4 (38) 2.3: Apr
Centrocercus urophasianus (bird) 1 (18) 4.0: Nov
Chordeiles minor (bird) 1 (5) 2.0: Aug
Eremophila alpestris (bird) 2 (84) 2.5: Apr Nov
Junco oreganus (bird) 1 (30) 11.0: Oct
Lanius ludovicianus (bird) 1 (20) 1.0: Apr
Leucosticte tephrocotis (bird) 1 (25) 3.0: Nov
Dipodomys ordii 1 (808) 5.0: Oct
 * *Lepus californicus* 5 (125) 4.6: Dec
Perognathus parvus 1 (474) 1.0: May
Peromyscus maniculatus 1 (1866) 6.0: Aug
Sylvilagus nuttallii 2 (28) 3.0: Oct Dec
- Euschoengastia sciuricola* (May-Oct) 7 1a
Eutamias minimus 2 (398) 2.0: Oct
Marmota flaviventris 1 (6) 3.0: May
- Euschoengastia* sp. (Aug-Oct) 19 1a
Dipodomys ordii 3 (808) 1.0: Aug Oct
Microtus montanus 1 (25) 8.0: Aug
Perognathus parvus 2 (474) 2.5: Aug
Peromyscus maniculatus 2 (1866) 1.5: Sep Oct
- Haemogamasus ambulans* (Mar-Oct) 8 dny 1 ♂ 80 ♀
 * *Dipodomys ordii* 10 (808) 1.4 - ♀: Jun Jul
Eutamias minimus 1 (398) 1.0 - dny: Mar
 * *Onychomys leucogaster* 6 (63) 5.7 - dny ♂ ♀: Jun-Aug Oct
Perognathus parvus 2 (474) 1.0 - ♀: Jun Aug
 * *Peromyscus maniculatus* 31 (1866) 1.2 - ♀: Mar Jun-Aug Oct
Reithrodontomys megalotis 1 (39) 1.0 - ♀: Aug
Thomomys talpoides 1 (8) 1.0 - dny ♀: ?
- Haemogamasus longitarsus* (Jun) 7 ♀
 * *Onychomys leucogaster* 3 (63) 1.0
Peromyscus maniculatus 4 (1866) 1.0
- Haemolaelaps casalis* (Jun-Oct) 1 ♀ 1 ?
Perognathus parvus 1 (474) 1.0: Oct
Peromyscus maniculatus 1 (1866) 1.0: Jun
- Haemolaelaps glasgowi* (Jan-Nov) 26 pny 64 dny 57 ♂ 1062 ♀
Eremophila alpestris (bird) 1 (84) 1.0 - ♀: Mar
 * *Dipodomys ordii* 72 (808) 2.1 - pny dny ♂ ♀: Mar-Aug Oct Nov
 * *Eutamias minimus* 24 (398) 4.9 - pny ♀: Mar Jun-Oct
- Microtus montanus* 7 (25) .1 - ♂ ♀: Jan Jun-Aug Nov
 * *Onychomys leucogaster* 36 (63) 5.4 - pny dny ♂ ♀: Mar Apr Jun-Oct
 * *Perognathus parvus* 33 (474) 2.8 - pny dny ♂ ♀: Apr-Oct
 * *Peromyscus maniculatus* 281 (1866) 2.1 - pny dny ♂ ♀: Jan-Nov
Plecotus townsendii 1 (78) 5.0 - ♀: Apr
Reithrodontomys megalotis 1 (39) 1.0 - ♀: Aug
Spermophilus townsendii 9 (60) .3 - ♀: Apr-Jul
Thomomys talpoides 1 (8) 1.0 - ♀: Jun
- Haemolaelaps* sp. (Mar-Jun) 1 pny 1 ♂
Dipodomys ordii 1 (808) 1.0 - ♂: Mar
Peromyscus maniculatus 1 (1866) 1.0 - pny: Jul
- Hirstionyssus bisetosus* (Sep) 2 ♀
Neotoma cinerea 1 (14) 2.0
- Hirstionyssus hilli* (Mar-Aug) 17 ♀
Eutamias minimus 1 (398) 1.0: Jul
Onychomys leucogaster 1 (63) 1.0: Mar Jun
 * *Perognathus parvus* 5 (474) 2.6: May Jul Aug
Peromyscus maniculatus 2 (1866) 1.0: Jul Aug
- Hirstionyssus incomptus* (Mar-Nov) 91 ♀
 * *Dipodomys ordii* 37 (808) 21.0: Mar Jun-Oct
Eutamias minimus 1 (398) 1.0: Jun
Perognathus parvus 2 (474) 2.0: Jun Jul
Peromyscus maniculatus 6 (1866) 1.2: Jun-Aug Nov
- Hirstionyssus isabellinus* (Nov) 1 ♀
Microtus montanus 1 (25) 1.0
- Hirstionyssus longichelae* (Jun-Oct) 6 ♀
Dipodomys ordii 1 (808) 1.0: Jun
Peromyscus maniculatus 1 (1866) 1.0: Jun
 * *Thomomys talpoides* 2 (8) 2.0: Jun Oct
- Hirstionyssus neotomae* (Sep-Oct) 48 ♀
Eutamias minimus 1 (398) 4.0: Oct
Neotoma cinerea 1 (14) 44.0: Sep
- Hirstionyssus thomomys* (Mar-Oct) 7 ♀
Onychomys leucogaster 1 (63) 1.0: Jul
Peromyscus maniculatus 1 (1866) 1.0: Sep
 * *Thomomys talpoides* 3 (8) 1.7: Mar Jun Oct
- Hirstionyssus triacanthus* (Apr-Oct) 185 ♀
Sceloporus graciosus (lizard) 1 (314) 1.0: Sep
Chordeiles minor (bird) 2 (5) 1.5: Aug
Dipodomys ordii 111 (808) 2.4: Apr-Oct
Eutamias minimus 5 (398) 1.0: Jul Oct
Neotoma cinerea 1 (14) 1.0: Sep
Perognathus parvus 2 (474) 2.0: Jun Jul
Peromyscus maniculatus 5 (1866) .8: Jun-Aug
Spermophilus townsendii 2 (60) 1.0: Jun

- Hirstionyssus utahensis* (Mar-Nov) 54 ♀
Dipodomys ordii 2 (808) 1.5: Jun Aug
 * *Eutamias minimus* 9 (398) 2.8: Jul Aug
Onychomys leucogaster 1 (63) 1.0: Jun
Perognathus parvus 5 (474) 1.0: Jun Jul
 * *Peromyscus maniculatus* 74 (1866) .3: Mar Jun-Sep Nov
Spermophilus townsendii 1 (78) 1.0: Jul
- Hirstionyssus* sp. (Mar-Oct) 71 dny 36 ♂ 14 ♀
Dendrocopos villosus (bird) 1 (1) 1.0 - ♂: ?
Dipodomys ordii 18 (808) 2.9 - dny ♂ ♀: Jun-Oct
Eutamias minimus 5 (389) 1.4 - dny ♂: Jun Jul Sep Oct
Microtus montanus 1 (25) 1.0 - dny: ?
Neotoma cinerea 2 (14) 4.0 - dny ♂ ♀: ?
Onychomys leucogaster 1 (63) 1.0 - dny ♀: Mar Apr
Perognathus parvus 6 (474) .7 - dny ♂ ♀: May-Aug
Peromyscus maniculatus 23 (1866) .8 - dny ♂ ♀: Jun-Aug
Thomomys talpoides 3 (8) 4.0 - dny ♂: ?
- Hypoaspis lubrica* (Aug) 1 ♀
Perognathus parvus 1 (474) 1.0
- Ischyropoda armatus* (May-Oct) 3 dny 25 ♂ 186 ♀
Crotalus viridis (snake) 1 (95) 1.0 - ♀: Sep
 * *Dipodomys ordii* 33 (808) 1.1 - ♂ ♀: Jun-Sep
Lepus californicus 1 (125) 1.0 - dny: Oct
Microtus montanus 3 (25) .7 - ♀: Jul Aug
 * *Onychomys leucogaster* 23 (63) 3.0 - dny ♂ ♀: Jun-Oct
 * *Perognathus parvus* 14 (474) 1.0 - ♂ ♀: May-Sep
 * *Peromyscus maniculatus* 61 (1866) 1.3 - dny ♂ ♀: May-Oct
Sorex merriami 1 (9) 7.0 - ♀: Aug
Thomomys talpoides 1 (8) 1.0 - ♀: Oct
- Ischyropoda furmani* (Jan-Aug) 3 ♂ 25 ♀
 * *Dipodomys ordii* 9 (808) 1.2 - ♀: Jun-Aug
Onychomys leucogaster 2 (63) 1.0 - ♀: Aug
Perognathus parvus 5 (474) 2.6 - pny dny ♂ ♀: Jun-Aug
Peromyscus maniculatus 9 (1866) 1.0 - ♂ ♀: Jan Jun-Aug
- Ischyropoda* sp. (Apr-Sep) 5 pny 55 dny 14 ♂ 23 ♀
Dipodomys ordii 7 (808) 2.3 - pny dny ♂ ♀: Jun-Sep
Eutamias minimus 3 (398) 1.0 - dny ♀: Aug Oct
Neotoma cinerea 1 (14) 2.0 - dny ♂ ♀: Jun Aug
Onychomys leucogaster 7 (63) 5.6 - dny ♂ ♀: Jun Aug
Perognathus parvus 5 (474) 2.6 - pny dny ♂ ♀: Jun-Aug
- Peromyscus maniculatus* 15 (1866) 1.4 - pny dny ♂ ♀: Jan Jun-Aug
Sorex merriami 1 (9) 3.0 - dny: Aug
Spermophilus townsendii 1 (60) 1.0 - dny: Apr
- Kleemania* sp. (Apr-Sep) 154 ♀
Chordeiles minor (bird) 1 (5) 1.0: Aug
 * *Dipodomys ordii* 8 (808) 6.5: Jun-Sep
Eutamias minimus 1 (398) 1.0: Jul
Microtus montanus 1 (25) 12.0: Aug
Neotoma cinerea 1 (14) 1.0: Sep
 * *Onychomys leucogaster* 5 (63) 3.8: Jun-Aug
 * *Perognathus parvus* 7 (474) 4.3: Apr Jun-Sep
 * *Peromyscus maniculatus* 32 (1866) 1.2: Jun-Sep
Sorex merriami 1 (9) 1.0: Aug
- Lecuwenhoekia americana* (Jul) 6 1a
Dipodomys ordii 1 (808) 6.0
- Listrophorus* sp. (Mar-Nov) 960
Chordeiles minor (bird) 1 (5) 1.0: Aug
 * *Dipodomys ordii* 53 (808) 18.1: Mar-May Aug-Nov
Peromyscus maniculatus 1 (1866) 2.0: Jun
- Macronyssus unidens* (Feb-Mar) 1 1a 1 pny 1 dny 1 ♂ + others
Plecotus townsendii 35 (78) ?
- Odontacarus linsdalei* (Jul) 6 1a
Dipodomys ordii 1 (808) 6.0
- Odontacarus micheneri* (Jul) 10 1a
Dipodomys ordii 1 (808) 10.0
- Ornithonyssus bacoti* (Oct) 1 ♀
Dipodomys ordii 1 (808) 1.0
- Ornithonyssus sylviarum* (Jul-Sep) 16 ♀
Amphispiza belli (bird) 2 (38) 2.0: Jul
Oreoscoptes montanus (bird) 1 (13) 2.0: Jul
 * *Poocetes gramineus* (bird) 3 (13) 1.3: Jul
Zonotrichia leucophrys (bird) 1 (33) 4.0: Sep
- Radfordia bachai* (Aug) 1 1a
Dipodomys ordii 1 (808) 1.0
- Trombicula arenicola* (Jul-Oct) 325 1a
Dipodomys ordii 26 (808) 12.5
- Trombicula bakeri* (Jul-Aug) 21 1a
Dipodomys ordii 1 (808) 21.0
- Trombicula belkini* (Jul-Aug) 167 1a
Phrynosoma douglassi (lizard) 1 (19) 7.0: Aug
 * *Sceloporus graciosus* (lizard) 19 (314) 8.4: Jul Aug

Trombicula doremi (Jul-Aug) 98 1a

- * *Dipodomys ordii* 24 (808) 3.6: Jul Aug
- Onychomys leucogaster* 1 (63) 1.0: Aug
- Perognathus parvus* 5 (474) 2.0: Aug

Trombicula sp. (Aug-Oct) 12 1a

- Sceloporus graciosus* (lizard) 1 (314) 1.0: Aug
- Dipodomys ordii* 3 (808) 3.0: Aug Oct
- Onychomys leucogaster* 1 (63) 1.0: Aug
- Peromyscus maniculatus* 1 (1866) 1.0: Aug

Louse-Host Associations

Enderleinellus sp. (prob. *suturalis*) (Apr-Oct) 1 ♂ 3 ♀

- Perognathus parvus* 1 (434) 1.0 - ♀: Oct
- Peromyscus maniculatus* 1 (1866) 1.0 - ♂: Aug

- * *Spermophilus townsendii* 2 (60) 1.0 - ♀: Apr Jul

Fahrenholzia pinnata (Mar-Nov) 63 ♂ 137 ♀

- Sceloporus graciosus* (lizard) 1 (314) 1.0 - ♀: Aug

- * *Dipodomys ordii* 86 (808) 1.8 - ♂ ♀: Mar Apr Jun-Nov

- Eutamias minimus* 4 (398) 1.5 - ♂ ♀: Jun Jul Oct

- * *Perognathus parvus* 15 (474) 1.6 - ♂ ♀: May-Aug Oct

- Peromyscus maniculatus* 11 (1866) 1.4 - ♂ ♀: Apr Jun-Sep

- Sylvilagus idahoensis* 1 (13) 1.0 - ♂: Nov

Fahrenholzia sp. (prob. *pinnata*) (Jun-Oct) 1 ♂ 4 ♀ 47 im 1 ?

- * *Dipodomys ordii* 27 (808) 1.0 - ♀ im: Jun-Aug
- Eutamias minimus* 1 (398) 1.0 - im: Jul

- Onychomys leucogaster* 1 (63) 1.0 - im: Jun
- Perognathus parvus* 6 (474) 2.2 - ♂ ♀: im: May-Aug Oct

- Peromyscus maniculatus* 2 (1866) 2.0 - im ? : Jun-Jul Oct

Geomydoecus sp. (Oct) 4 ♂ 9 ♀ 2 im

- Thomomys talpoides* 1 (8) 15.0

Haemodipsus setoni (Feb-Jul) 21 ♂ 28 ♀ 18 im

- Lepus californicus* 2 (125) 12.0 - ♂ ♀ im: May Jul

- Peromyscus maniculatus* 1 (1866) 1.0 - ♀: Mar

- * *Sylvilagus nuttallii* 2 (28) 21.0 - ♂ ♀ im: Feb

Hoplopleura acanthopus (Mar-Aug) 8 ♂ 20 ♀

- Microtus montanus* 6 (25) 4.7

Hoplopleura arboricola (Mar-Oct) 136 ♂ 257 ♀ 1 im

- Sceloporus graciosus* (lizard) 1 (314) 2.0 - ♀: Sep

- Ereunetes mauri* (bird) 1 (6) 1.0 - ♀: Aug

- Dipodomys ordii* 2 (808) 3.5 - ♂ ♀: Mar Jul

- * *Eutamias minimus* 83 (398) 4.0 - ♂ ♀: Mar May-Aug Oct

- Marmota flaviventris* 2 (6) 1.0 - ♂: Jun

- Perognathus parvus* 1 (474) 5.0 - ♂ ♀: Aug

- Peromyscus maniculatus* 16 (1866) 2.1 - ♂ ♀: Mar Jun-Aug

- Spermophilus townsendii* 2 (60) 4.0 - ♂ ♀ im: Jun-Jul

Hoplopleura erratica (Jul-Oct) 1 ♂ 4 ♀

- * *Eutamias minimus* 4 (398) 1.0 - ♂ ♀: Jul-Aug Oct

- Perognathus parvus* 1 (474) 1.0 - ♀: Jul

Hoplopleura hesperomydis (Jan-Dec) 16 ♂ 440 ♀

- Ereunetes mauri* (bird) 1 (6) 8.0 - ♂ ♀: Mar Jun Aug

- Dipodomys ordii* 7 (808) 1.3 - ♂ ♀: Jun Aug

- Eutamias minimus* 7 (398) 1.1 - ♂ ♀: Mar Jun Aug

- Microtus montanus* 2 (25) 1.0 - ♂ ♀: Jun Aug

- Onychomys leucogaster* 1 (63) 1.0 - ♀: Jul

- Perognathus parvus* 3 (474) 2.0 - ♂ ♀: Aug

- * *Peromyscus maniculatus* 167 (1866) 3.4 - ♂ ♀: Jan-Dec

- Reithrodontomys megalotis* 1 (39) 2.0 - ♂ ♀: May

Neohaematopinus inornatus (Aug) 2 ♂ 2 ♀

- Neotoma cinerea* 2 (14) 2.0

Neohaematopinus laeviusculus (Apr-Aug) 68 ♂ 107 ♀ 60 im

- Eutamias minimus* 2 (398) 1.0 - ♂: Jul-Aug

- Marmota flaviventris* 2 (6) 1.0 - ♀: May

- Perognathus parvus* 1 (474) 2.0 - ♂ ♀: Jul

- Peromyscus maniculatus* 5 (1866) 2.8 - ♂ ♀: Mar-Jun Aug

- * *Spermophilus townsendii* 26 (60) 8.5 - ♂ ♀ im: Apr-Jul

Neohaematopinus marmota (Apr-Aug) 25 ♂ 26 ♀ 13 im

- * *Marmota flaviventris* 4 (6) 14.0 - ♂ ♀ im: May-Jun

- Peromyscus maniculatus* 4 (1866) 2.3 - ♂ ♀: Apr Aug

Neohaematopinus pacificus (May-Nov) 21 ♂ 46 ♀

- * *Eutamias minimus* 27 (398) 2.1 - ♂ ♀: May-Aug Oct Nov

- Perognathus parvus* 2 (474) 1.5 - ♂: Jul

- Peromyscus maniculatus* 4 (1866) 1.8 - ♂ ♀: Feb Mar Aug

- Reithrodontomys megalotis* 1 (39) 1.0 - ♀: Aug

- Spermophilus townsendii* 1 (60) 2.0 - ♀: Jul

Neohaematopinus sp. (Aug) 1 ?

- Dipodomys ordii* 1 (808) 1.0

Neotrichodectes interruptofasciatus (Apr-Nov) 19 ♂
15 ♀ 23 im
Taxidea taxus 2 (5) 28.5

Polyplax auricularis (Jan-Dec) 331 ♂ 669 ♀
Sceloporus graciosus (reptile) 2 (314) 1.0 - ♂:
Sep
Ereunetes mauri (bird) 1 (6) 1.0 - ♀: Aug
Dipodomys ordii 4 (808) 1.0 - ♂ ♀: Jul-Aug Nov
Eutamias minimus 7 (398) 1.0 - ♂ ♀: Mar Jun-
Aug
Neotoma cinerea 1 (14) 1.0 - ♀: Jun
Perognathus parvus 2 (474) 1.0 - ♀: Jun Aug
* *Peromyscus maniculatus* 224 (1866) 4.3 - ♂ ♀:
Jan-Dec
* *Spermophilus townsendii* 5 (60) 1.0 - ♂ ♀: Apr
Jun-Jul
Sylvilagus nuttallii 1 (28) 1.0 - ♀: Aug

Polyplax spinulosa (Jul) 1 ♂
Microtus montanus 1 (25) 1.0

Polyplax sp. (Jun-Jul) 2 ♀
Microtus montanus 2 (25) 1.0

Mallophaga (Jan-Oct) 35 ♂ 70 ♀ 68 im 6 ?
Buteo regalis (bird) 1 (4) 24.0 - ♂ ♀ im: Aug
Centrocercus urophasianus (bird) 2 (18) 2.5 - ♀
im: Jul

Circus cyaneus (bird) 1 (1) 1.0 - im: Apr
Didodomys ordii 3 (808) 1.0 - ? : Apr Sep-Oct
Eremophila alpestris (bird) 1 (84) 4.0 - ♂ ♀: Jul
Ereunetes mauri (bird) 4 (6) 2.5 - ♀ im: Mar
Jun-Aug
Eutamias minimus 6 (398) 3.2 - ♀ im: Mar Jun-
Aug
Falco sparverius (bird) 1 (6) 1.0 - ♂: Jun
Junco oreganus (bird) 1 (30) 1.0 - im: Apr
Lepus californicus 1 (125) 9.0 - ♂ ♀: Apr
Lynx rufus 1 (8) 2.0 - im: Jan
Oreoscoptes montanus (bird) 1 (13) 1.0 - ♀: Jul
Perognathus parvus 5 (474) 3.4 - ♂ ♀ im: ? :
Apr-May Jul-Aug
Peromyscus maniculatus 9 (1866) 1.9 - ♂ ♀ im:
Mar-May Jul-Aug
Pica pica (bird) 1 (8) 1.0 - im: Feb
Plecotus townsendii 1 (78) 4.0 - im: Apr
Reithrodontomys megalotis 1 (39) 15.0 - ♂ ♀
im: Apr
Sceloporus graciosus (lizard) 1 (314) 3.0 - ♀ im:
Jun
Spermophilus townsendii 5 (60) 7.6 - ♂ ♀ im:
Apr-Jun
Spinus pinus (bird) 1 (23) 1.0 - ? : Jun
Sterna neglecta (bird) 1 (7) 1.0 - im: Jul
Zenaidura macroura (bird) 1 (23) 2.0 - ♂ im:
Jul

HOST-PARASITE RELATIONSHIPS

(* = the mite and/or louse which occurred most commonly on that host; H = new host record based on replications—other associations listed may represent new records, but are not so indicated because of infrequent occurrence considered accidental infestations or contaminations).

Reptiles

Crotalus viridis
Eubrachyla elaps debilis
Ischyropoda armatus
Phrynosoma douglassi
Trombicula belkini
Sceloporus graciosus
Hirstionyssus triacanthus
* *Trombicula belkini*
Fahrenheitia pinnata
Hoplopleura arboricola
Polyplax auricularis
Mallophaga

Birds

Amphispiza belli
* *Euschoengastia radfordi*
Ornithonyssus sylviarum
Asyndesmus lewis
Dermanyssus gallinae

Buteo regalis
Mallophaga
Centrocercus urophasianus
Eubrachyla elaps debilis
* *Euschoengastia radfordi*
Mallophaga
Circus cyaneus
Mallophaga
Chordeiles minor
Euschoengastia radfordi
Hirstionyssus triacanthus
Klemania sp.
Listrophorus sp.
Dendrocopos villosus
* *Dermanyssus gallinae*
Hirstionyssus sp.
Eremophila alpestris
Bernia marita
* *Dermanyssus gallinae*
Euschoengastia radfordi
Haemolaelaps glasgowi
Mallophaga
Ereunetes mauri
Hoplopleura arboricola
H. hesperomydis
Polyplax auricularis
Mallophaga

Falco sparverius
 Mallophaga
Junco oreganus
Euschoengastia radfordi
 Mallophaga
Lanius ludovicianus
Euschoengastia radfordi
Leucosticte tephrocotis
Euschoengastia radfordi
Oreoscoptes montanus
Ornithonyssus sylviarum
 Mallophaga
Pica pica
 Mallophaga
Piranga ludoviciana
Dermanyssus sp.
Poocetes gramineus
Ornithonyssus sylviarum
Salpinctes obsoletus
Euschoengastia oregonensis
Spinus pinus
 Mallophaga
Sternella neglecta
 Mallophaga
Turdus migratorius
Dermanyssus gallinae
Zenaidura macroura
 Mallophaga
Zonotrichia leucophrys
Euschoengastia decipiens
 * *Ornithonyssus sylviarum*

Mammals

Dipodomys ordii
Androlaelaps leviculus
Dermanyssus sp.
Eubrachylaelaps crowei
E. debilis
Euschoengastia cordiremus
 * *E. decipiens*
E. radfordi
Haemogamasus ambulans
 * *Haemolaelaps glasgowi*
 * *Hirstionyssus incomptus*
H. longichelae
H. triacanthus
H. utahensis
 * *Ischyropoda armatus*
I. furmani
 * *Klemania* sp.
Leeuwenhoekia americana
 * *Listrophorus* sp.
Odontacarus linsdalei
O. micheneri
Ornithonyssus bacoti
Radfordia bachai
 * *Trombicula arenicola*

T. bakeri
 * *T. doremi*
 * *Fahrenholzia pinnata*
Fahrenholzia sp.
Hoplopleura arboricola
H. hesperomydis - H
Neohaemotopinus sp.
Polyplax auricularis
 Mallophaga
Eutamias minimus
Androlaelaps leviculus
Euschoengastia decipiens - H
E. fasolla
E. pomerantzi
E. schuricola
Haemogamasus ambulans
 * *Haemolaelaps glasgowi*
Hirstionyssus hilli
H. incomptus
H. neotomae
H. triacanthus - H
H. utahensis
Ischyropoda sp. - H
Klemania sp.
Fahrenholzia pinnata
Fahrenholzia sp.
 * *Hoplopleura arboricola*
H. erratica
H. hesperomydis - H
Neohaematopinus laeviusculus
 * *N. pacificus*
Polyplax auricularis - H
 Mallophaga
Lepus californicus
Euschoengastia decipiens
E. luteodema
 * *E. radfordi*
Ischyropoda armatus
Haemodipsus setoni
 Mallophaga
Lynx rufus
 Mallophaga
Marmota flaviventris
Euschoengastia sciuricola
Hoplopleura arboricola
Neohaematopinus laeviusculus
 * *N. marmotae*
Microtus montanus
Euschoengastia sp.
 * *Haemolaelaps glasgowi*
Hirstionyssus isabellinus
Ischyropoda armatus - H
Klemania sp.
 * *Hoplopleura acanthopus* - H
H. hesperomydis
Polyplax spinulosa
Polyplax sp.
Neotoma cinerea

- Brevisterna* sp.
Chatia ochotona
Euschoengastia decipiens
Hirstionyssus bisetosus
 * *H. neotomae*
H. triacanthus
Ischyropoda sp.
Kleemania sp.
 * *Neohaematopinus inornatus* - H
Polyplax auricularis
Onychomys leucogaster
Androlaelaps leviculus
 * *Eubrachylaelaps crowei*
E. debilis - H
Haemogamasus ambulans
H. longitarsus - H
 * *Haemolaelaps glasgowi*
Hirstionyssus hilli
H. thomomys
H. utahensis
 * *Ischyropoda armatus*
I. furmani
Kleemania sp.
Trombicula doremi
Fahrenholzia sp.
Hoplopleura hesperomydis
Perognathus parvus
Androlaelaps sp.
Dermanyssus gallinae
Eubrachylaelaps debilis - H
 * *Euschoengastia decipiens*
E. radfordi
Haemogamasus ambulans
Haemolaelaps casalis
 * *H. glasgowi*
 * *Hirstionyssus hilli*
H. incomptus
H. triacanthus
H. utahensis - H
Hypoaspis lubrica
 * *Ischyropoda armatus*
I. furmani - H
 * *Kleemania* sp.
Trombicula doremi - H
Enderleinellus sp.
 * *Fahrenholzia pinnata*
Fahrenholzia sp.
Hoplopleura arboricola
H. erratica
H. hesperomydis
Neohaematopinus laeviusculus
N. pacificus
Polyplax auricularis
Mallophaga
Peromyscus maniculatus
Androlaelaps leviculus
Bernia marita
Eubrachylaelaps circularis
E. crowei
 * *E. debilis*
Euschoengastia cordiremus
E. criceticola
 * *E. decipens*
E. lanei
E. radfordi
 * *Haemogamasus ambulans*
H. longitarsus
Haemolaelaps casalis
 * *H. glasgowi*
Hirstionyssus hilli
H. incomptus
H. longichelae
H. thomomys
H. triacanthus
 * *H. utahensis*
 * *Ischyropoda armatus*
I. furmani
 * *Kleemania* sp.
Listrophorus sp.
Trombicula sp.
Enderleinellus sp.
Fahrenholzia pinnata - H
Fahrenholzia sp.
Haemodipsus setoni
Hoplopleura arboricola - H
 * *H. hesperomydis*
Neohaematopinus laeviusculus
N. marmotae
N. pacificus
 * *Polyplax auricularis*
Mallophaga
Plecotus townsendii
Chatia ochotona
Haemolaelaps glasgowi
 * *Macronyssus unidens*
Mallophaga
Reithrodontomys megalotis
Haemogamasus ambulans
Haemolaelaps glasgowi
Hoplopleura hesperomydis
Neohaematopinus pacificus
Mallophaga
Sorex merriami
Ischyropoda armatus
Kleemania sp.
Spermophilus townsendii
 * *Haemolaelaps glasgowi*
Hirstionyssus triacanthus
H. utahensis
Ischyropoda sp.
Enderleinellus sp.
Hoplopleura arboricola
 * *Neohaematopinus laeviusculus*
N. pacificus
Polyplax auricularis
Mallophaga

Sylvilagus idahoensis
 Euschoengastia decipiens
 Fahrenheitia pinnata
Sylvilagus nuttallii
 * *Euschoengastia decipiens*
 E. radfordi
 * *Haemodipsus setoni*
 Polyplax auricularis
Taxidea taxus

Neotrichodectes interruptofasciatus
Thomomys talpoides
 Euschoengastia decipiens
 Haemogamasus ambulans
 Haemolaelaps glasgowi
 Hirstionyssus longichelae
 * *H. thomomys*
 Ischyropoda armatus
 Geomydoecus sp.

ECOLOGICAL CONSIDERATIONS

Degree of Host Infestation

The degree of infestation of mammals differed relative to their geographic distribution (Table 1).
A greater percentage of *Peromyscus maniculatus* was infested with mites in Area 12 than in other areas, with the lowest percentages in Areas 6, 10 and 11. *Perognathus parvus* in Areas 1 and 5 were the most heavily infested, whereas those in Area 7 were the least. In Area 5 *Eutamias minimus* were heavily infested, whereas in Area 3 none were infested. The greatest infestation rate for *Dipodomys ordii* was in Area 8 and the lowest in Area 4. Except in Area 5, no two species of mammals in the same area had a high

rate of infestation with mites. The same was true for the lowest rates of infestation.
A greater percentage of *Dipodomys ordii* was infested with lice in Areas 6 and 8, and fewer animals in Areas 5 and 10 were infested than in other areas. The greatest percentage of infested *Eutamias minimus* was in Areas 2 and 10, and fewest in Area 7. No significant differences were noted for *Perognathus parvus* except in Areas 7, 9 and 10, where no infested animals were found even though 108 were examined. A greater percentage of *Peromyscus maniculatus* was infested in Area 4, and fewer infested animals were found in Area 11 than in other areas. On the basis of frequency and degree of infestation, the areas where louse infestation was optimum for *Dipodomys ordii*

Table 1. Percentage of hosts¹ infested with mites and lice in each of 12 major study areas.

Host	% ² of hosts infested in each study area ³											
	1	2	3	4	5	6	7	8	9	10	11	12
MITES												
<i>Dipodomys ordii</i>	71		50	45	58	87		97	77	71	89	53
<i>Eutamias minimus</i>	10	6	0		24		6			4		
<i>Perognathus parvus</i>	35	16	21		38		15	24		20		
<i>Peromyscus maniculatus</i>	42	32	60		45	14	50	26	45	18	18	79
LICE												
<i>Dipodomys ordii</i>	17		17	12	6	21		23	8	6	16	14
<i>Eutamias minimus</i>	20	32	24		24		6			40		
<i>Perognathus parvus</i>	8	8	3		8		0	3		0		
<i>Peromyscus maniculatus</i>	27	29	23		30	12	18	22	11	12	8	21

¹Only those hosts that were widely distributed geographically are included.
²To nearest whole percent.
³Data not included when less than 10 hosts from the area were examined.

are 6, 8 and 11, for *Eutamias minimus* 2 and 3, and for *Peromyscus maniculatus* 2 and 5. Considering lice of all species, hosts in Area 2, 5 and 9 were more heavily infested than those in other areas.

In each of the 12 study areas, a greater percentage of the hosts belonging to *Dipodomys ordii*, *Perognathus parvus*, and *Peromyscus maniculatus* were infested with mites than with lice. The reverse situation occurred with *Eutamias minimus*. Four exceptions to these conditions wherein about equal percentages of hosts were infested with mites and lice were *Eutamias minimus* in Areas 5 and 7, and *Peromyscus maniculatus* in Areas 2 and 6.

Host Abundance and Species Variety

The number of species parasites which occurred on a particular kind of host generally was in direct proportion to the number of hosts examined (Table 2).

Table 2. Number of mammals examined and number of species of mites and lice found on each kind.

Host		No. species	
Species	No. examined	Mites	Lice
<i>Peromyscus maniculatus</i>	1866	25	9
<i>Dipodomys ordii</i>	808	25	5
<i>Perognathus parvus</i>	474	17	8
<i>Eutamias minimus</i>	398	14	7
<i>Lepus californicus</i>	125	4	1
<i>Plecotus townsendii</i>	78	3	0
<i>Onychomys leucogaster</i>	63	13	2
<i>Spermophilus townsendii</i>	60	4	5
<i>Reithrodontomys megalotis</i>	39	2	2
<i>Sylvilagus nuttalli</i>	28	2	2
<i>Microtus montanus</i>	25	5	4
<i>Neotoma cinerea</i>	14	8	2
<i>Sylvilagus idahoensis</i>	13	1	1
<i>Sorex merriami</i>	9	2	0
<i>Thomomys talpoides</i>	8	6	1
<i>Marmota flaviventris</i>	6	1	3

Mammals of three species did not fit the expected ratio of direct proportion with reference to mites—*Peromyscus maniculatus* and *Sylvilagus idahoensis* had fewer species of mites than would be expected, and *Onychomys leucogaster* more species than expected. I assume that the numbers of *Peromyscus* examined approached the upper end of the “numbers examined—species present” ratio, whereas the unexpected ratios for *Sylvilagus* and *Onychomys* may be related to their behavior patterns and/or habitat.

Lice are more host specific than mites, fleas or ticks. Consequently the sucking lice in this study were more restricted in host distribution than fleas or mites, but followed the similar trend of number of

species found in direct proportion to number of hosts examined. Exceptions were *Plecotus townsendii* on which no lice were found, and *Spermophilus townsendii*, *Microtus montanus* and *Marmota flaviventris*, which possessed more species of lice than expected.

Degree of Infestation by Sex of Host

Some significant differences in the rate of infestation on mammals of different sexes were noted for parasites of some species (Table 3).

Table 3. Comparative rates of infestation by mites and lice on the different sexes of mammals of some species.

Parasite and host	Parasite-host index	
	♂ hosts	♀ hosts
Mites		
<i>Eubrachylaelaps crowei</i>		
<i>Onychomys leucogaster</i>	5.4	5.0
<i>Eubrachylaelaps debilis</i>		
<i>Peromyscus maniculatus</i>	2.2	3.3
<i>Euschoengastia decipiens</i>		
<i>Dipodomys ordii</i>	10.4	3.0
<i>Perognathus parvus</i>	19.9	4.0
<i>Peromyscus maniculatus</i>	6.0	5.2
<i>Haemogamasus ambulans</i>		
<i>Dipodomys ordii</i>	1.3	1.2
<i>Onychomys leucogaster</i>	3.5	2.4
<i>Peromyscus maniculatus</i>	1.2	1.3
<i>Haemolaelaps glasgowi</i>		
<i>Dipodomys ordii</i>	1.6	1.6
<i>Eutamias minimus</i>	1.8	7.3
<i>Microtus montanus</i>	1.6	1.1
<i>Onychomys leucogaster</i>	6.0	2.4
<i>Perognathus parvus</i>	1.8	2.9
<i>Peromyscus maniculatus</i>	1.8	1.6
<i>Spermophilus townsendii</i>	2.8	2.5
<i>Hirstionyssus incomptus</i>		
<i>Dipodomys ordii</i>	1.4	3.2
<i>Hirstionyssus triacanthus</i>		
<i>Dipodomys ordii</i>	2.6	2.5
<i>Hirstionyssus utahensis</i>		
<i>Eutamias minimus</i>	4.7	1.5
<i>Peromyscus maniculatus</i>	2.0	5.3
<i>Ischyropoda armatus</i>		
<i>Dipodomys ordii</i>	2.0	1.6
<i>Onychomys leucogaster</i>	2.6	2.5
<i>Perognathus parvus</i>	1.0	1.1
<i>Peromyscus maniculatus</i>	1.4	1.2
<i>Ischyropoda furmani</i>		
<i>Dipodomys ordii</i>	1.3	1.0

Table 3. (Continued)

Parasite and host	Parasite-host index	
	♂ hosts	♀ hosts
<i>Peromyscus maniculatus</i>	1.0	1.0
<i>Klemania</i> sp.		
<i>Dipodomys ordii</i>	2.1	2.5
<i>Peromyscus maniculatus</i>	1.6	1.0
<i>Listrophorus</i> sp.		
<i>Dipodomys ordii</i>	20.0	17.6
<i>Trombicula arenicola</i>		
<i>Dipodomys ordii</i>	9.0	1.2
<i>Trombicula belkini</i>		
<i>Sceloporus graciosus</i>	6.7	8.3
<i>Trombicula doremi</i>		
<i>Dipodomys ordii</i>	3.0	4.0
Lice		
<i>Fahrenholzia pinnata</i>		
<i>Dipodomys ordii</i>	2.0	1.6
<i>Hoplopleura arboricola</i>		
<i>Eutamias minimus</i>	4.7	4.0
<i>Hoplopleura hesperomydis</i>		
<i>Peromyscus maniculatus</i>	4.1	4.1
<i>Neohaematopinus laevisculus</i>		
<i>Spermophilus townsendii</i>	12.6	5.1
<i>Neohaematopinus pacificus</i>		
<i>Eutamias minimus</i>	2.4	1.4
<i>Polyplax auricularis</i>		
<i>Peromyscus maniculatus</i>	3.6	2.4

Males of *Dipodomys ordii* and *Perognathus parvus* were more heavily infested with mites of *Euschoen-gastia decipiens* than were females. Relative to mites of *Haemolaelaps glasgowi*, females of *Eutamias mini-mus* were more heavily infested, whereas the males of *Onychomys leucogaster* were more heavily infested. For *Hirstionyssus utahensis*, male *Eutamias minimus* were more heavily infested, whereas female *Peromys-cus maniculatus* were more heavily infested. Males of *Dipodomys ordii* were more heavily infested with mites of *Trombicula arenicola* than were females.

For the most part, a greater percentage of the male hosts were more heavily infested with lice than were the females. This was most evident with *Polyplax aur-icularis* on *Peromyscus maniculatus*. In every case but one (*Hoplopleura hesperomydis* on *Peromyscus mani-culatus*) the louse-host index was higher for males than for females, although the difference was not sig-nificant except for *Neohaematopinus laevisculus* on *Spermophilus townsendii*.

Seasonal Occurrence

Complete seasonal occurrences of the mites and lice are given in the listings in the sections "Mite-Host Associations" and "Louse-Host Associations." Their occurrence on commonly collected hosts is summar-ized in Tables 4 and 5.

I assume that a direct correlation exists between the number and kinds of hosts examined and the number of kinds of parasites found. This was true ex-cept for October when proportionately more species of mites and lice were found than would be expected from the number of hosts examined. The number of species of parasites taken during July and August were equal, although more hosts were examined in August than in July. The number of kinds of parasites in relationship to the number of kinds of hosts ex-aminated was in direct correlation for other months ex-cept for April, July and November when fewer kinds of mites, and in June when fewer lice were found than expected from the number of kinds of hosts ex-aminated. In February more kinds of lice were found than expected.

The absence of Mallophaga on so many birds was unusual, particularly on *Amphispiza belli*, *Lanius ludovicianus*, *Leucosticte tephrocotis*, and *Zono-trichia leucophrys*.

For the sucking lice an unusual situation was the apparent absence of these parasites during specific months. Lice were found on *Peromyscus maniculatus* every month, yet were absent on other of their com-mon hosts at times when one would expect them to be present. Significant examples of absence are in May for *Dipodomys ordii*, August and December for *Lepus californicus*, and September for *Perognathus parvus*.

Reproduction In Mites

An egg or larva was observed within the idiosoma of mites of seven species. Females of *Eubrachyla-laps crowei* were gravid with eggs during June, July, August and October, and with larvae from June to October, inclusive. Females of *E. debilis* contained eggs from February through December (except in September and October), and larvae during the same period except October. Mites of *Haemolaelaps glas-gowi* were gravid with eggs from March through October, and with larvae for the same period except in May and September. Mites of *Hirstionyssus hilli* contained eggs in August, those of *H. incomptus* in June and July, those of *H. neotomae* in September, and those of *H. thomomys* in October.

The cosmopolitan species *Haemolaelaps glasgowi*, which occurs on such a variety of hosts, was common on mammals of five species at the NRTS, but those taken from *Dipodomys ordii* contained the greatest

Table 4. Seasonal infestation of some common hosts¹ with mites² and lice.²

Host	No. vertebrates examined and parasites ³ present											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Reptiles												
<i>Crotalus viridis</i>					47	33	2	1	6	6		
						M			M			
<i>Sceloporus graciosus</i>				1	14	102	53	65	77	5		
							M	M	M			
Birds												
<i>Amphispiza belli</i>				15	8		5	2	8			
<i>Eremophila alpestris</i>	6	3	4	29	7	7	7	3	7	7	2	3
		M	M	M			L				M	
<i>Junco oreganus</i>			1	12					8	9		
				L						L		
<i>Lanius ludovicianus</i>			1	19								
<i>Leucosticte tephrocotis</i>	5	5									16	
<i>Spinus pinus</i>	3									1		17
						L						
<i>Zenaidura macroura</i>				2	14	5	2					
							L					
<i>Zonotrichia leucophrys</i>					6				26	1		
Mammals												
<i>Dipodomys ordii</i>			50	20	26	183	175	245	60	64	13	
			LM	LM	M	LM	LM	LM	LM	LM	LM	
<i>Eutamias minimus</i>			51	4	7	53	137	103	7	25	6	
			LM		L	LM	LM	LM	M	LM	L	
<i>Lepus californicus</i>	6		8	13	3	10	13	27	11	7	7	20
				LM	L		L			LM		M
<i>Microtus montanus</i>	8		1			1	5	7		2	1	
			L			L	L	L				
<i>Onychomys leucogaster</i>			7	1		15	13	14	5	6	1	1
			M	M		LM	LM	M	M	LM		
<i>Perognathus parvus</i>				14	66	117	122	130	19	6	1	
				LM	LM	LM	LM	LM	M	LM		
<i>Peromyscus maniculatus</i>	5	43	114	40	13	439	514	475	69	82	41	40
	LM	LM	LM	LM	LM	LM	LM	LM	LM	LM	LM	LM
<i>Reithrodontomys megalotis</i>			6	1	3	1	9	17		4		
				L	L			L				
<i>Spermophilus townsendii</i>			5	5	8	33	8					
				LM	LM	LM	LM					
<i>Sylvilagus nuttallii</i>		7	1		1	4	4	4	2	2	1	3
		L										

¹Only those are listed wherein a total of 20 or more animals were examined of those species which are common hosts for mites or lice.

²All species.

³L = lice, M = mites.

Table 5. Numbers of species of mites and lice collected each month relative to numbers and kinds of mammals.

Item	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. hosts examined	19	50	243	98	121	856	1001	1022	173	198	71	64
Kinds hosts examined	3	2	9	8	8	10	10	9	7	9	8	4
Kinds parasites found:												
Mites	3	4	13	8	10	19	25	25	16	21	8	4
Lice	2	4	8	7	8	8	11	11	4	8	5	2

percentage of gravid females (13%) when compared with those on *Peromyscus maniculatus* (7%), *Onychomys leucogaster* (5%), *Perognathus parvus* (4%), and *Eutamias minimus* (3%).

Consortism

Where sufficient numbers of parasites were found to make comparisons, different degrees of species consortism were noted (Table 6).

Mites of *Euschoengastia decipiens*, although found on a variety of hosts, were seldom in association with mites of other genera. All of the common species except *Trombicula arenicola* occurred as the only species of mite on their hosts in more than half the collections. *Euschoengastia radfordi*, *E. decipiens* and *Hirstionyssus incomptus* frequently were associated with other species of the same genus.

Consortism between lice of different species was not as common as with other ectoparasites. Lice of the species *Polyplax auricularis* occurred as the only

ones on their host a greater percentage of the time than did other lice. All of the commonly collected species except *Neohaematopinus pacificus* occurred as the only lice on their hosts in more than half of the collections. A significant correlation occurred with *N. pacificus* which was associated with *Hoplopleura arboricola* in 43 percent of its collections. A similar correlation was noted between *Hoplopleura hesperomydis* and *Polyplax auricularis*. Significant intrageneric associations were noted for *Hoplopleura* and *Neohaematopinus*.

Geographic Distribution

The distribution of parasites of most species was directly correlated with the distribution of the host on which the parasites were most commonly found. Of the mites, *Eubrachyla elaps debilis*, *Hirstionyssus incomptus*, *Listrophorus* sp. and *Trombicula arenicola* were more widely distributed than expected, and *Euschoengastia radfordi*, *Bernia marita* and *Ornithonyssus sylvianus* were more geographically restricted than were the hosts on which they were found.

Lice of the species *Neohaematopinus pacificus*, and especially those of *Hoplopleura erratica*, were more geographically restricted than the hosts on which they were most commonly found.

The numbers of species of mites and lice found in each study area are shown in Table 7. Although fewer species than expected were found in every area, the greatest deviations from the average numbers of species present were Areas 5 and 7 for the mites and Areas 4 and 8 for the lice.

Radiation Influence

Animals differed in their degree of infestation with ectoparasites in an irradiated area when compared with an ecologically similar nonirradiated one (Table 8).

Animals of *Eutamias minimus* and *Peromyscus maniculatus* were less frequently infested with mites in the irradiated area than in the nonirradiated one. The mite-host index was about equal for *Eutamias minimus* in the two areas, but was higher for *Peromyscus maniculatus* in the irradiated one.

Fewer species of lice were found, a smaller percentage of mammals were infested, and a lower louse-host index for *Eutamias minimus* occurred in the irradiated area. Although the louse-host index was lower for *Peromyscus maniculatus*, a higher percentage of the mammals were infested and more species of lice were found in the irradiated area.

Unusual Host Records

Routine processing of many animals for ectoparasites creates a potential for error and contamination

Table 6. Frequency of intrageneric and species associations for some commonly collected mites and lice.

Parasite	% ¹ of times found:	
	As only species ² on host	With species of same genus
Mites		
<i>Trombicula belkini</i>	100	0
<i>Euschoengastia radfordi</i>	94	17
<i>Hirstionyssus incomptus</i>	84	11
<i>Klemania</i> sp.	83	0
<i>Eubrachyla elaps debilis</i>	80	1
<i>Haemogamasus ambulans</i>	79	0
<i>Euschoengastia decipiens</i>	79	11
<i>Listrophorus</i> sp.	77	0
<i>Hirstionyssus utahensis</i>	77	5
<i>Trombicula doremi</i>	75	6
<i>Ischyropoda armatus</i>	67	2
<i>I. furmani</i>	67	8
<i>Hirstionyssus triacanthus</i>	66	4
<i>Haemolaelaps glasgowi</i>	55	1
<i>Trombicula arenicola</i>	39	9
Lice		
<i>Polyplax auricularis</i>	73	0
<i>Fahrenholzia pinnata</i>	67	0
<i>Hoplopleura arboricola</i>	64	9
<i>Hoplopleura hesperomydis</i>	60	18
<i>Neohaematopinus laevisculus</i>	53	6
<i>Neohaematopinus pacificus</i>	34	6

¹Nearest whole percent.
²Of mites or of lice, respectively.

even though the greatest care is exercised. Consequently, many of the host records in the list of host-parasite relationships must be considered as tentative, especially when they represent only one or two collections. On the other hand, some of the records represent sufficient replications to be valid, and consequently must be considered as new. These are *Euschoengastia decipiens*, *Hirstionyssus triacanthus* and *Ischyropoda* sp. on *Eutamias minimus*; *Ischyropoda armatus* on *Microtus montanus*; *Eubrachylaelaps debilis* and *Haemogamasus longitarsus* on *Onychomys leucogaster*; and *E. debilis*, *Hirstionyssus utahensis*, *Ischyropoda furmani* and *Trombicula doremi* on *Perognathus parvus*.

Table 7. Numbers of species of mites and lice found in the major study areas in proportion to the kinds and numbers of hosts examined.

Study Area	No. hosts examined ¹		No. species mites		No. species lice	
	Individuals	Species	Expected ²	Found	Expected ²	Found
1	169	6	45	18	12	6
2	155	4	29	13	10	5
3	311	7	25	12	12	7
4	40	3	25	9	9	3
5	117	4	41	12	10	5
6	51	3	41	13	10	6
7	57	4	25	14	10	5
8	148	5	41	14	10	7
9	93	3	41	13	9	5
10	39	4	45	17	10	5
11	39	4	41	13	10	4
12	49	3	41	15	10	5

¹Only those are included that are known to be common hosts of mites or lice.
²Based on number and kinds of hosts examined in relationship to parasites found on these hosts in at least one other study area.

Table 8. Differences in degree of infestation by mites and lice on mammals of two species in irradiated and nonirradiated areas.

Area	No. hosts examined	% hosts infested with:		No. species present		Parasite-host index	
		Mites	Lice	Mites	Lice	Mites	Lice
<i>Eutamias minimus</i>							
38 (control)	18	67	39	4	7	1.2	13.1
13 (irradiated)	20	30	30	4	4	1.5	1.7
<i>Peromyscus maniculatus</i>							
37 (control)	22	95	14	5	2	.6	11.0
13 (irradiated)	80	50	26	9	4	26.0	4.3

New records for lice, which likely are not contaminations, are *Fahrenholzia pinnata* on *Peromyscus maniculatus*, *Hoplopleura acanthopus* on *Microtus montanus*, *H. arboricola* on *P. maniculatus*, *H. hesperomydis* on *Dipodomys ordii* and *Eutamias minimus*, and *Polyplax auricularis* on *E. minimus*.

Taxonomic Considerations of the Lice

I have taken the liberty to include some applicable comments made by Dr. William T. Jellison relative to his identifications of the lice.

Enderleinellus sp.—These probably were of ground squirrel origin, and likely are *E. suturalis*.

Fahrenholzia pinnata.—This is a characteristic parasite of *Dipodomys*. The specimens from *Perognathus*

were only tentatively relegated to this species by Jellison. On the Idaho specimens the upper left-hand pleural plate is consistently longer than on typical *F. pinnata*.

Haemodipsus setoni.—Lice relegated to this species were taken from *Lepus* and *Sylvilagus*. A different species likely occurs on each of these hosts, but so far no distinction has been recognized.

Hoplopleura erratica.—Western chipmunks have two louse parasites—*H. erratica arboricola* and *Neohaematopinus pacificus*. The Idaho specimens are closer to the subspecies *H. e. erratica*, typical of *Tamias*, than to the western *H. c. arboricola*.

Polyplax auricularis.—This typically infests *Peromyscus* and mice of several other genera, and Jellison seriously questions the records from *Dipodomys*, *Perognathus* and *Spermophilus*.

DISCUSSION

Community Relationships

In the 12 major study areas where collections were made during all seasons, the degrees of infestation of each species of hosts were not consistent between different areas. However, in Areas 7 and 10 the degree of infestation was lower for more species than for the other areas. The same predominant plants were present in Areas 7 and 10 and in some of the other areas, but total composition and edaphic differences likely exist which affect parasite infestation of the host as well as its nest.

Species Variety

For those ectoparasites that are not considered host specific, the number of species of ectoparasites found on a particular species of host was proportionate to the number of hosts examined. The fewer kinds of mites than expected to be found on *Peromyscus maniculatus* is unusual in consideration of the abundance, distribution and habits of these rodents. The greater number of species of mites than expected on *Onychomys leucogaster* is not unusual in light of its carnivorous habits. The unusual number of species of lice on *Spermophilus*, *Microtus* and *Marmota* is unexpected because of the apparent host specificity of these ectoparasites and the habitat and behavior of their hosts.

Sexual Differences

Where degree of infestation according to sex of host differed for a given species, the males were more often and more heavily infested than the females, although this varied somewhat with the species of parasite. This may be related to the reproductive, nesting and food-getting activities of the different hosts. The greater degree of infestation of males is contrary to

an assumption that females are potentially apt to be more heavily infested because they spend more time associated with the nest because of their reproductive activities. The nest is assumed to be the principle reservoir of many ectoparasites of the nest-building rodents. On the other hand, the wandering activities of the males may provide for greater potential contact with ectoparasites seeking a host. Furthermore, the nest itself may contain plant materials and dusts which act as pesticides against the ectoparasites.

Seasonal Occurrence

The summer months (July and August) are expected to represent the optimum period for the greatest number of species of ectoparasites on the hosts inasmuch as this is the time when populations of hosts are attaining their peak, and environmental conditions should be optimum for ectoparasite reproduction. The decline in September and subsequent increase in October likely is related to the maturation of immatures produced by the mid-summer adults. The expected decline in winter months occurred for the mites, but populations of lice in February were higher than expected. This latter situation may be due to the optimum environmental conditions of the nest as a result of animal hibernation, or decreased amounts of activity outside of the nest.

Consortism

Whether the degree of consortism is directly related to the species of ectoparasite involved or to edaphic or other environmental factors is not known. For the lice, considered as being more host specific than the mites, individual species seldom occurred with other lice, especially with those of the same genus. Although mites of different species frequently

were associated together, those of two species represented the extremes of consortism. Chigger mites of *Euschoengastia decipiens* seldom were found in association with other mites, whereas the mesostigmatid *Eubrachylaelaps crowei* was almost always found in association with other species. The occurrence of mites of two species of the same genus on the same host was not considered common in proportion to the number of times each species was found, but was much more common in the mites than with the lice.

Geographic Distribution

One may assume that the distribution of an ectoparasite should be in direct relationship to the distribution of its common hosts, especially with the lice where host specificity is more evident than with the mites. Such was the case with most of those mites and lice studied. Based on host relationships, however, mites of three species were more widely distributed than expected, whereas those of three other species were more restricted than expected. Undoubtedly environmental factors other than the host are influential on these mites. No correlation with a

predominant type of vegetation was evident, and highest and lowest populations were found in two communities which contained the same species of predominant plants. On the other hand, other species which occurred in greatest numbers were associated with plant associations wherein greater cover and organic debris were present.

Radiation Effects

The effects of radiation, *per se*, on the rate of ectoparasite infestation are not known. However, in one disturbed area fewer ectoparasites occurred than in an ecologically similar undisturbed area. This situation occurred for lice and mites on *Eutamias minimus*, but was different for ectoparasites on *Peromyscus maniculatus*. Although fewer mice were infested with mites in the irradiated area than in the undisturbed area, the mite-host index was higher. Exactly the reverse situation occurred with lice on *P. maniculatus*. I believe that the differences in rates of infestation are not due to the effects of radionuclides, but rather to the physical disturbance of the habitat, i.e., destruction of plants and soil manipulation.

SUMMARY

Mites of 47 species and lice of 16 species were taken from reptiles of 3 species, birds of 23 species, and mammals of 18 species at the National Reactor Testing Station between June, 1966, and September, 1967. Mammals differed in degree of infestation relative to their geographic distribution at the station. The number of species of ectoparasites which occurred on a particular kind of host generally was in direct proportion to the number of hosts examined, but exceptions occurred in some instances. In some cases the rate of infestation differed relative to the sex of the host. The greatest numbers of species of mites and lice were found during July and August, fewest species of mites from December through Feb-

ruary, and fewest kinds of lice during December and January. Host preferences for mites of some species were evident during their reproductive and nonreproductive periods. Consortism among the ectoparasites differed in degree by species. Except for mites of seven species and lice of two species, the geographic distribution of the ectoparasites was in direct proportion to the distribution of the host on which they were commonly found. Mammals of two species differed in their frequency of infestation with ectoparasites in an irradiated area when compared to an ecologically similar nonirradiated control area. Ten new host records for mites and six for lice were established.

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**A COMPARATIVE STUDY OF THE HEAD AND
THORACIC OSTEOLOGY AND MYOLOGY OF THE
KINKS *EUMECES GILBERTI* VAN DENBURGH AND
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and

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A COMPARATIVE STUDY OF THE HEAD AND THORACIC
OSTEOLOGY AND MYOLOGY OF THE SKINKS,
EUMECES GILBERTI VAN DENBURGH, AND *EUMECES*
SKILTONIANUS (BAIRD AND GIRARD)

by

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INTRODUCTION

A. F. Weigmann (1834) described the genus *Eumeces* in *Herpetologica mexicana* and *E. parvimentatus* (Geoffroy-St. Hillaire) was designated genotype.

The two species involved in this study belong to the *skiltonianus* group which are characterized by the presence of two dorsolateral and two lateral light lines on the body. *Eumeces skiltonianus* is found in British Columbia, Idaho, Montana, Utah, Nevada, northern Arizona, California, and Baja California. Baird and Girard (1852) described *E. skiltonianus* and designated Oregon as the type locality.

Van Denburgh (1896) described a new species from southern California which he called *Eumeces gilberti*. Camp, (1916) disagreed with the distinctness of this new species and considered all western skinks to belong to the same species, *skiltonianus*. Since the publication of Camp's paper the distinctness of these two species has been verified by more thorough investigations, which have been based on geographical distribution, size, color pattern, scale counts, and other external morphological characters. Taylor (1935) was the first to do a complete study of the genus *Eumeces* and he recognized these two species; Smith (1946) further characterized them in his *Handbook of Lizards*; and Rodgers and Fitch (1947) set forth the distribution of *gilberti* and the distinguishing characters of that species. Tanner (1957) charac-

terized *skiltonianus*, designated its type population, and described two new subspecies. The papers of Rodgers and Fitch, and Tanner set forth the external anatomical characteristics of these species. They also recognized that all subspecies of *skiltonianus* exhibit a striped pattern; whereas, only the immature forms of *gilberti* have the striped pattern. Adults of *gilberti* are patternless and much larger than the adults of *skiltonianus*; the average snout-vent length for *gilberti* is about 88 mm and for *skiltonianus* about 64 mm. The studies of external taxonomic characters of these two species seem to be complete; therefore, it is the purpose of this study to further clarify their taxonomic and phylogenetic relationships by comparing and examining the osteology and myology of their head and thorax regions.

Extensive literature reviews on general and specific osteology and myology have been done by other authors: Robison and Tanner (1962), Oelrich (1956), Avery and Tanner (1964), Jenkins and Tanner (1968), and Fisher and Tanner (1970). Only those references which are relevant to this report are given. The skulls of ten species within the genus *Eumeces* including *gilberti*, were compared by Kingman (1932). To date the only myological work within this genus available to the author is the publication by Edgeworth (1935), in which he describes *E. schmidleri*.

Materials and Methods

The subspecies used in this study are *E. gilberti placerensis* (5), *E. g. rubricaudatus* (3), *E. skiltonianus skiltonianus* (10), and *E. s. utahensis* (5).

The specimens of *E. gilberti* have the following numbers: Brigham Young University (31956-58 inclusive, 32622, and 32623); Sacramento State College (303, 437, and 528). The specimens of *E. skiltonianus* have the following numbers: Brigham Young University (8721, 12467, 12468, 12472, 12474, 13750, 13756, 21939, and 31959-65 inclusive).

Osteological material was prepared by skinning the specimens, removing the superficial muscles using forceps, placing the specimens in a 50% liquid bleach solution for 30 to 60 seconds and rinsing them afterwards in clear water. The last three procedures were alternated until the desired results were obtained. Care was taken not to destroy the osteological elements when removing the muscles with forceps nor to leave the specimens in the bleach solution for an extended length of time. Illustrations were produced

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by photographing the skulls through a binocular scope using 400 ASA, 35 mm black and white film. The pictures were then enlarged to ten inches and traced onto mylar tracing sheets using a binocular scope for detail.

A full description of each skeletal element of *E. gilberti* is given under "G." If differences in *skiltonianus* are noted, they are given under "S." A minimum of five skulls of each species is used for the description and comparative differences. All elements are discussed in alphabetical order.

Preserved specimens were carefully skinned for myological comparisons. Illustrations were obtained by taking measurements from the preserved specimens, enlarging them onto tracing paper, and then transferring them onto mylar tracing sheets.

A full description of each muscle for *E. gilberti* is given under "G." If differences in *skiltonianus* are noted, they are given under "S." A minimum of four specimens of each species is used for the description and comparative differences. All elements are discussed in alphabetical order.

OSTEOLOGY

General Description of the Skull

Generally the skull is delicate and for the most part completely ossified. The extremities are bounded by the rostrum, the occipital condyle, and the quadrates laterally. The rostrum is rounded and contains large narial openings which are bounded by the premaxillae, the nasals, and the prefrontals. The articulation between the nasals and the frontals marks an area of abrupt change in elevation with the frontals being higher. Anterodorsally the frontals contact the maxillae thus preventing the nasals from articulating with the prefrontals. The frontals form the medial margin of the orbits; whereas, the prefrontals and postfrontals form the anterior and posterior margins of the orbits respectively. The parietal is slightly rugose and contains a centrally located parietal foramen. Its posterior margin is dorsoventrally slanted and has two lateral and two medial processes. The postorbitals articulate with the jugals either separately or in conjunction with the postfrontals. In some specimens the postorbitals are reduced to such an extent that only a small slender bone remains. The squamosals, however, do not come in contact with the jugals. A supratemporal fontanelle located posteriorly is bordered by the parietal, postfrontal, postorbital and squamosal elements. The occipital and otic regions are posteroventral to the parietal and are generally highly fused. The fusion of elements does not always correspond directly with the size of the skull. The supraoccipital forms an ascendens process with the parietal. The basioccipital is generally fused with the other occipital elements, with the basisphenoid and also with the prootics. The parasphenoid is a slender pointed element attached to the ventral border of the interorbital septum and extends anteriorly. The anteromedial limb of the pterygoids contains a number of pleurodont teeth. The palatines contact only the maxillae, vomers, and pterygoids. Two pairs of Jacobson's organs are housed in the vomers. The jugals have small spines extending posteriorly on their lateroventral margins. The maxillae and premaxillae contain cylindrical pleurodont teeth. The

right premaxilla is larger and contains one more tooth than the left premaxilla. Two orbital fenestrae, two infraorbital fenestrae, two infratemporal fenestrae, and two posttemporal fenestrae are located in the skull.

Description of the Skull Elements

Basioccipital. (Figs. 2 and 3)

G. The basioccipital contributes to the cranium floor, is roughly hexagonal in shape, and forms the basal portion if not all of the occipital condyle. Kingman (1932) reported that the exoccipitals formed the lateral portions of the occipital condyle. In the specimens studied, however, fusion obscures the possible presence of sutures with the exoccipitals. Articulation with the basisphenoid anteriorly and the prootics laterally are generally by fusion. If sutures are present, the basioccipital-basisphenoid suture is irregular and the basioccipital-prootic suture extends posteriorly and then dorsally, separating the prootic and opisthotic portions of the otic capsule and terminating on the ventral margin of the fenestrae ovali. The prominent basioccipital processes project ventrolaterally and in some cases have an epiphysis. These processes appear to be formed in part by the exoccipital and the paroccipital elements. Anterior to the above processes smaller protuberances are found which make up part of the otic capsules.

Basisphenoid. (Fig. 3)

G. The basisphenoid contributes to the anterior portion of the cranial floor. Anteriorly it contacts the parasphenoid. Anterolaterally the basiptyergoid processes emerge and enlarge distally into flangelike processes which articulate with the pterygoids by a cartilaginous pad. Lateral contact is generally made with the prootics by fusion of the two elements. The sella turcica is posterior to the basiptyergoid processes. A small foramen located on the lateral surface of the basisphenoid forms a canal with the prootics.

Ectopterygoid. (Figs. 1 and 3)

G. The ectopterygoids have dorsal and ventral processes which enclose the lateral processes of the pterygoids. Contact is also made with the maxillae and jugals. These bones do not articulate with the palatines.

Epiotic. (Not figured)

G. The epiotics are part of the otic capsule and enclose the dorsal parts of the two vertical semicircular canals (Jollie, 1960). They appear as large rounded protuberances when viewed from the foramen magnum and extend medially and dorsally. They fuse inside the braincase with the supraoccipital, the opisthotics, the paroccipital processes, and the exoccipitals.

Epipterygoid. (Fig. 2)

G. The epipterygoids are relatively straight ossified rods extending from a well developed socket on the dorsal margin of the pterygoids to the anterior descending processes of the parietal and posterior descending processes of the prootics. They have a slight lateral cant ventrodorsally.

Exoccipital. (Fig. 2)

G. The exoccipitals form the ventrolateral margins of the foramen magnum. They are fused with the supraoccipital dorsally and the basioccipital ventrally. Fusion in this area makes it difficult to determine if these bones contribute to the occipital condyle. Laterally they fuse with the paroccipital processes. Anteriorly they form the posterior margin of the fenestrae rotunda. One, two, or three hypoglossal nerve foramina are located in the exoccipitals near the junction with the paroccipital processes. The jugular foramina are bordered by these latter two bones.

Frontal. (Figs. 1, 2, and 3)

G. The frontal element forms the cranial roof between the orbits. The anterior lateral processes of the frontal always contact the maxillae. Posteriorly articulation is with the postfrontals and parietal. The suture with the parietal is slightly convex. The descending processes in the orbits are slender and contact the dorsal palatine limbs medial to the prefrontals.

S. Anteriorly this bone articulates with the nasals, prefrontals, and may contact the maxillae depending upon the extent of the anterior lateral processes of the frontal.

Interorbital Ossification. (Fig. 2)

This is an ossified element found in both species, and which is connected anteriorly to the internasal septum. It extends posterior and slightly ventral, and is found within the interorbital septum. In one speci-

men of *E. gilberti* this element extends posteriorly as far as the braincase. In both species it varies from short to long and from triangular to almost rectangular in shape.

Jugal. (Figs. 1, 2, and 3)

G. The jugals form the lateroventral margin of the orbits and the anterior margin of the infratemporal fenestrae. Their dorsoposterior margin generally articulates with the postfrontals and always with the postorbitals. They do not contact the squamosals. These bones articulate with the ectopterygoids ventrally. On their lateroposteroventral surface is a short posterior spine. Kingman (1932) states that this projection suggests "the place of continuance of some element in the past." Anteroventrally the jugals are sandwiched between the lateral and medial processes of the maxillae.

Lacrimal. (Figs. 1 and 2)

G. The lacrimals are small rectangular splints of bone forming a portion of the ventroanterior margin of the orbits between the prefrontals and the maxillae. They are not always fused with the prefrontals. On their posteroventral surface there is an arch of this element forming one to two foramina which lead into the large lacrimal duct anteriorly.

Maxilla. (Figs. 1, 2, and 3)

G. The maxillae are the tooth-bearing bones of skull with from 15 to 20 teeth per side, and an average of 19. Replacement teeth are present. The teeth are pleurodont. The medial surface is level with the palatine. The teeth are cylindrical, homodont, rounded at the tips, and extend slightly laterally. Dorsally the maxillae articulate with the nasals and with the frontals posteriorly. Anteriorly in the narial openings the maxillae send a slender process inward to meet the anterior process of the septomaxillae. The maxillae articulate with the premaxillae in the floor of the narial openings, and on the ventroanterior surface of the skull they overlap the lateral processes of the premaxillae. Posteriorly, articulation is with the prefrontals, the lacrimals, and the jugals. Ventrally, the maxillae articulate with the premaxillae and the vomers anteriorly, the palatines medially by the posterior palatine processes, the jugals posteriorly, the ectopterygoids medially, and the prefrontals in the anterolateral portion of the orbits. The maxillae are not always fused with the lacrimals. The lateral surfaces of the maxillae contain six to eight supralabial foramina of varying sizes and shapes.

S. The maxillae may or may not contact the frontal posteriorly. They have a range of 17 to 20 teeth per side, with an average of 18 and contain four to seven supralabial foramina.

Nasal. (Figs. 1 and 2)

G. The nasals cover most of the anterior dorsal surface of the skull. They contact the premaxillae and the narial openings anteriorly, the maxillae laterally, the frontal posteriorly, and do not articulate with the prefrontals. Three to five nasal foramina are present, the posterior one being located near the junction of the prefrontals, nasals, and frontal elements. Sutures with the frontal are highly irregular and lobed.

S. The nasals may or may not contact the prefrontals. Two to four nasal foramina are generally present. The suture with the frontal is not as irregular as that of *gilberti* unless articulation of the prefrontal and nasal elements is absent.

Opisthotic. (Fig. 1)

G. The opisthotics form the posterior portion of the otic capsule; the anterior portion being formed by the prootics (Smith, 1960). A suture separating these two bones terminates at the ventral margin of the fenestrae ovali. On the dorsal surface the opisthotics are fused with the epiotics and the prootics. The posterior portion of the opisthotics or the paroccipital processes connect the occipital region to the quadrate region. These processes are wide and generally fuse with the supratemporals and the quadrates and posteroventrally they contact the prootics.

Os Palpabra. (Fig. 1)

G. The os palpabrae are irregular tear-shaped bones which are attached to the dorsal posterior margin of the prefrontals by connective tissue.

Palatine. (Figs. 1, 2, and 3)

G. The palatines have a ventral and a dorsal limb. Posteriorly these two limbs join each other and articulate with the medial limb of the pterygoids. The ventral limbs articulate with the maxillae by the posterior palatine processes. The dorsal limbs are arched upward forming the wall of the internal nares and contact the descending processes of the frontals and the prefrontals. Anteriorly this limb articulates with the vomers. The dorsal limbs contact each other for about one-fourth their length before separating posteriorly to join the ventral limbs. The separated halves form a slight ventral ridge. The palatine canals are located in the ventral limbs just medial to the articulation with the maxillae.

Parasphenoid. (Figs. 1 and 2)

G. This element is a cartilaginous tapered rod extending in an anterior direction from the center of the basisphenoid and forming the ventral border of the interorbital septum.

Parietal. (Figs. 1, 2, and 3)

G. The parietal is a large posterior dorsal element which articulates with the frontal anteriorly and the

postfrontals and the postorbitals laterally. The latter articulation is not present if the supratemporal fontanelle separates these two elements. The postero-lateral processes contact the squamosals, the supratemporals, the paroccipital processes, the opisthotics, and the prootics. Medially two shorter processes extend posterior and lateral to the ascendens process of the supraoccipital forming a metakinetic type of articulation (Romer, 1956). The posterior edge of the parietal including the medial and lateral processes slant ventrally with the result that the main body of the parietal is higher than the dorsal occipital region. The lateral borders of the parietal are slightly curved inward. Ventrally the descending wall laminae are drawn out and articulate with the anterodorsal border of the epipterygoids. A parietal foramen lies on the median line near the center of the bone. Articulation with the quadrate is absent.

Postfrontal. (Figs. 1 and 2)

G. The postfrontals contribute to the posterior margin of the orbits. Articulation is with the parietal medially and frontals anteriorly. Laterally contact is made with either the postorbitals or the postorbitals and the jugals. The suture with the postorbitals may be fused in some places.

Postorbital. (Figs. 1, 2, and 3)

G. The postorbitals vary in width and length, and frequently show a reduction of relative size when compared to other adjacent bones. They are found lateral to the postfrontals and medial to the squamosals. Anteriorly they articulate with the jugals and the postfrontals. The suture with the postfrontals may be fused in some places. Posteriorly these elements may articulate with the parietal depending upon the size of the supratemporal fontanelle. They do not articulate with the supratemporals.

S. The postorbitals vary in size, but are only occasionally reduced to the same degree as in *gilberti*.

Prefrontal. (Figs. 1 and 2)

G. The prefrontals articulate with the frontals medially and with the maxillae laterally. These elements have a large anterior orbital process which descends to contact the palatines, the frontals, and the lacrimals. In the anterior ventral portion of the orbit, articulation is made with the maxillae dorsally. A small foramen is either located in the descending process of the prefrontals or between the prefrontals and frontals.

S. The prefrontals articulate with the frontals medially, but may or may not articulate with the nasals.

Premaxilla. (Figs. 1, 2, and 3)

G. The right premaxilla is the larger and contains four pleurodont teeth as compared with three teeth

on the left element. This unequalness is produced by the extension of the midline suture into the left element. These elements may be fused in places. The premaxillae border the narial openings medially and the maxillae and vomers ventrally.

Prootic. (Figs. 1, 2, and 3)

G. The prootics are very complex elements forming a major portion of the cranium and the otic capsules. Ventrally they articulate, sometimes by fusion, with the basisphenoid and the basioccipital. If these elements are not fused, the suture continues posterior to the ventral margin of the fenestrae ovali. The lateroventral portion of the prootics is thin and deeply concave. The lateral wall of the prootics contain a canal which comes from the basisphenoid and continues to the otic capsule. Posteroventrally fusion is made with the paroccipital processes. The anterior descending processes contact the postero-dorsal margin of the epipterygoids.

Pterygoid. (Figs. 1, 2, and 3)

G. The pterygoids are "Y" shaped bones slightly less than one-half the length of the skull. The anterior limbs are large, heavy, and articulate with the palatines by an overlapping suture. These limbs have a depression in the center containing four to ten pleurodont teeth. The teeth are attached to the lateral side, face somewhat medially, may be in a single row, or in irregular groups; and they are more sharply pointed and smaller than those found elsewhere. The lateral limbs are sandwiched between the ventral and dorsal processes of the ectopterygoids. At the junction of these two bones the lateral surface of the pterygoids is flanged into the coronoid process. The posterior limbs curve inward anteriorly and then outward posteriorly to articulate with the quadrate, and then extend slightly beyond the quadrate articulation. In the middle of the pterygoids the basipterygoid processes articulate by a cartilaginous pad. Dorsal to the basipterygoid processes there is a socket into which the epipterygoids fit. Anterior to these processes, the pterygoids are highly concave medially and posterior to the above processes the pterygoids are highly convex medially.

Quadrate. (Figs. 1, 2, and 3)

G. The quadrates are large units articulating with the squamosal, supratemporal, and paroccipital elements posteriorly; and with the pterygoids anteriorly. The articulating surface with the pterygoids is saddle shaped.

Septomaxilla. (Fig. 1)

G. The septomaxillae are inverted cup-shaped structures lying dorsal to Jacobson's organ and extending anteriorly. They contact the premaxillae and the maxillae in the floor of the narial openings. There

is a thin ridge of bone extending upward and outward from the anterior portion of the septomaxillae which is joined by an inward process from the maxillae.

Stapes. (Fig. 3)

G. The stapes are thin cylindrical bones with flared bases which fit into the fenestrae ovali. The lateral ends are somewhat expanded. These bones are directed posterolaterally and extend into the quadrate region.

Supraoccipital. (Fig. 1)

G. The supraoccipital forms the superior margin of the foramen magnum and generally fuses with the exoccipitals ventrally. Laterally they fuse with the opisthotics and with the epiotics inside the braincase. A slight midsagittal ridge is formed and the ascendens process extends posteriorly under the parietal and forms a metakinetic articulation with the medial posterior processes of the parietal.

Supratemporal. (Figs. 1, 2, and 3)

G. The supratemporals are small slender bones wedged between the squamosals and the parietal dorsally. Ventrally they contact the quadrates and the paroccipital processes.

Squamosal. (Figs. 1, 2, and 3)

G. The squamosals are larger than the postorbitals and have a medial expansion of variable width. They are separated from the jugals by the postorbitals, and posteriorly they curve laterally and downward to articulate into a small depression of the quadrate. Posterior articulation is with the supratemporals and the parietal.

Vomer. (Fig. 3)

G. The vomers form the anteroventral surface of the skull. They are rolled laterally with the medial area being the more ventral. They are separated from each other by a deep medial longitudinal groove centrally. Anteriorly they become flat, constricted, and articulate with the premaxillae and the maxillae. They articulate posteriorly with the palatines. Anterior to the latter articulation two ventrally projected toothlike structures are present. The right and left halves are for the most part fused along their entire length. Each half contains one pair of Jacobson's organs.

General Description of the Mandible

Since the mandibles of these two species are similar except for the differences described below, figures of both species are not given. *E. skiltonianus* (Fig. 4) was chosen because of the superior illustration, and is typical for either species.

Each ramus is slightly bowed laterally. The rami

are united anteriorly by the mental symphysis and articulate posteriorly with the quadrates. An open sulcus of Meckel's cartilage is located on their ventromedial surface. Each ramus consists of seven elements; the angular, the articular, the coronoid, the dentary, the prearticular, and the surangular. The surfaces are smooth. The dentary bears a single row of pleurodont teeth. The retroarticular processes are thin and spoonshaped. The prearticulars are generally fused with the articulars.

Description of the Mandible Elements

Angular. (Fig. 4)

G. The angular is located on the ventral surface of the mandibular ramus. It is projected dorsally in an anteroposterior direction. On the lateral surface of the ramus it contacts the surangular dorsally, the dentary anteriorly, and the prearticular posteriorly. On the medial surface of the ramus the angular articulates by a forward splint of bone between the dentary and the splenial elements. Dorsally, articulation is with the prearticular. This element contains a small foramen anteriorly.

Articular. (Fig. 4)

G. The articular forms the articulating surface of the mandible for the quadrate. This element is an ossification of Meckel's cartilage and is bordered by dermal elements. The articular process extends medially. The articular is generally fused with the surangular dorsally and with the prearticular ventrally. It does not contact the angular.

Coronoid. (Fig. 4)

G. The coronoid is an inverted "V" shaped element which is centrally located and projects dorsally. It has one lateral and two medial processes. The lateral process contacts the surangular ventrally and the dentary anteriorly. The anterior medial process lies along the posterior portion of the dentary. The posterior medial process contacts the surangular and the prearticular. Between the two medial processes a well developed coronoid fossa is found which contains anterior portions of the surangular and prearticular. These two latter elements are sometimes fused.

Dentary. (Fig. 4)

G. The dentary is the tooth-bearing bone of the mandible. This element extends posteriorly to a distance equal to the posterior medial process of the coronoid. Nineteen to 23 pleurodont teeth, with an average of 21, are located on the dorsal surface of the dentary. Meckel's cartilage is open ventrally and is equal in length to no more than one-half that of the dentary. The dentary contacts the splenial at the posterior end of Meckel's cartilage. Anterior articulation is with the anterior process of the coronoid,

the surangular, and the angular. The lateral surface contains 3 to 6 mental foramina of various sizes and shapes.

S. The dentary contains 18 to 22 teeth, with an average of 21, and contains 3 to 7 mental foramina.

Prearticular. (Fig. 4)

G. The prearticular is a major component of the medial surface of the ramus. It is generally fused with the articular posteriorly and sometimes fused with the surangular dorsally. Ventrally it comes in contact with the angular. This element forms the retroarticular process of the ramus. The mandibular fossa is located posteriorly and is formed by the surangular dorsally and the prearticular ventrally.

Splenial. (Fig. 4)

G. The splenial lies on the medial anterior portion of the ramus, ventral to the dentary. It sends forward two small bones which enclose the posterior portion of the open sulcus of Meckel's cartilage prior to articulation with the dentary. This element extends posterior to the posterior margin of the posterior medial process of the coronoid. The splenial contains a foramen just posterior to the open portion of Meckel's cartilage.

Surangular. (Fig. 4)

G. Laterally the surangular covers the dorsal portion of the ramus between the dentary and the articular. It is generally fused with the articular posteriorly and forms the anterior portion of the articular process. It contacts the coronoid dorsally, the dentary anteroventrally, and the angular ventrally. On the medial surface it is sometimes fused with the prearticular. Posteriorly it contributes to the mandibular fossa with the prearticular. On the lateral surface two foramina are located.

Description of the Hyoid Apparatus

The general morphology of the hyoid apparatus in both species is similar. Variations, however, were noted in the average ratios of the length of the entoglossal process to either the length of the proximal segment of the hyoid cornu or the length of the ceratobranchial 2, with *gilberti* being greater in both cases. A sufficient number of specimens was not available for statistical analyses. The hyoid apparatus is represented by *E. gilberti* in Figure 5.

Hyoid Apparatus. (Fig. 5)

G. Unless stated differently, all elements are cartilaginous and highly calcified. The main body or the corpus is prolonged anteriorly into the entoglossal process. The latter is imbedded in the tongue musculature. The remainder of the corpus has two posterolateral projections which are connected to the other

elements. The hyoid cornu consists of two segments. The posterior portion of the proximal segment is almost completely ossified and articulates between the corpus and the ceratobranchial 1. The remainder of this segment is tubular and connects to the distal segment of the hyoid cornu. The distal segment is initially flat and wide; it then becomes thicker and somewhat tubular, and distally it again becomes flatter. This segment has a calcified core throughout

its length. The ceratobranchial 1 is completely ossified except near its articulation with its epibranchial. Medially it articulates with the proximal segment of the hyoid cornu. Initially it is tubular, toward the center it becomes wider, and distally it is tubular again and has a flared articulation with its epibranchial. The epibranchial is a slender and pointed element. The ceratobranchial 2 is tubular and fused indistinguishably to the corpus.

MYOLOGY

General Description of the Myology

This description reflects the general myological condition of both species. Differences are discussed later.

Ventrally the intermandibularis anterior is subdivided, interdigitates with the geniohyoideus, and is continuous with the intermandibularis posterior. The sternohyoideus is separable into a superficial and a profundus layer; the medial border is partially separated from its partner by an elliptical space. This space is covered by fascia; but when uncovered, portions of the trachea, thyroid gland, clavodeltoideus, and the clavicle can be seen. The pectoralis is a large muscle covering the sternum and the scapula; posteriorly this muscle interdigitates with the rectus abdominus. Ventrolaterally the pectoralis is covered by an anterior slip of the rectus abdominus which extends almost to the insertion of the pectoralis. A ligamentous fascia covers a large portion of the pectoralis and is connected to the anterior slip of the obliquus abdominus rectus posteriorly, to the lateral process of the interclavicle, and to the muscles immediately anterior to this process. There is only one mandibulo-hyoideus present. Both the clavodeltoideus and the coracobrachialis longus have a dorsal and a ventral origin on the clavicle and the scapula respectively. In the adductor muscle complex, the adductor mandibularis externus medius, the adductor mandibularis externus profundus, and the adductor mandibularis posterior are at equal depth. The second of these muscles extends through the posttemporal fenestrae to partially originate from the opisthotic and prootic elements. No levator anguli oris is present. The depressor mandibularis inserts on the retroarticular process and intermandibularis posterior, and in some specimens is separable into two bundles. The trapezius varies in thickness and in some specimens can also be separated into two bundles. The trapezius and the sternocleidomastoideus interdigitate ventrally to insert along with the sternohyoideus onto the interclavicle lateral process. There is both an anterior and a posterior scapulohumeralis. The obliquus abdominus externus muscle is divided into a superficial and a profundus layer. Dorsally the rectus capitis posterior

is separated into an anterior and a posterior bundle; the former has a medial and a lateral slip. The obliquus capitis magnus and the longissimus cervicis are joined to the spinalis capitis by a myosepta. No longissimus capitis is present.

Description of the Myology

M. Adductor Mandibularis Externus Medius. (Figs. 6, 8, and 10)

G. This muscle is deep to the adductor mandibularis externus superficialis from which it is separated with difficulty. It lies dorsal to the adductor mandibularis externus profundus and is separated anteriorly from this muscle by a tendon from the bodenaponeurosis. These two muscles interdigitate posteriorly. The muscle originates from the prootic and opisthotic elements deep to the spinalis capitis and lies between the medial and lateral slips of the rectus capitis posterior. The muscle fibers extend in a lateral direction and as they enter the posttemporal fenestrae turn anteroventrally, and have other origins from the beveled surface of the parietal, ventral surfaces of squamosals, postorbitals, jugals, and the dorsal surface of the quadrates. The fibers converge anteriorly to insert onto the coronoid by way of the bodenaponeurosis.

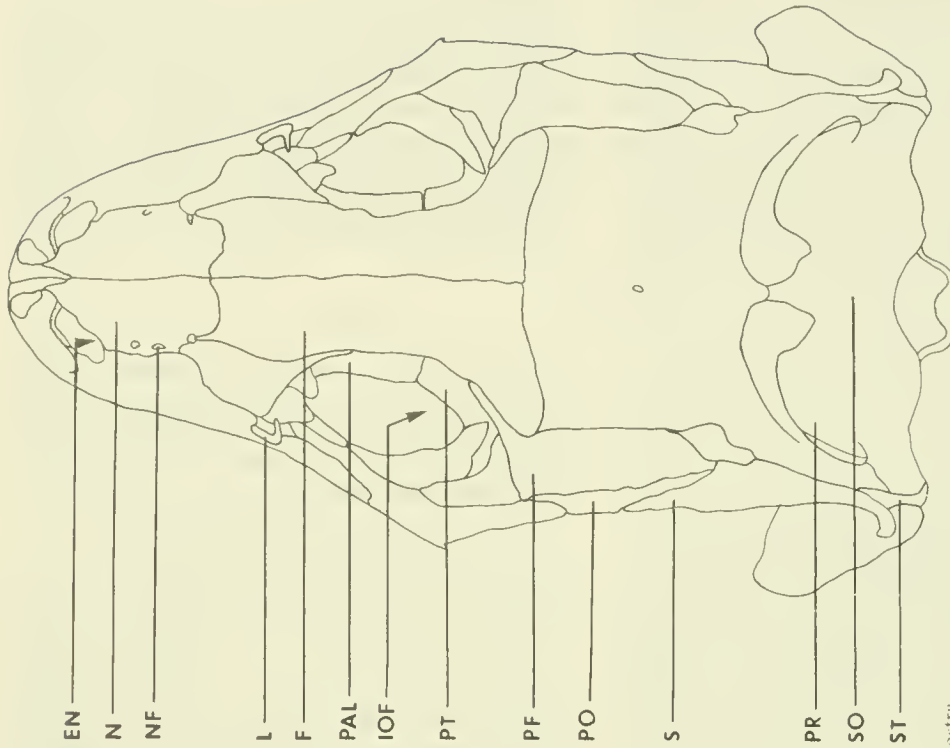
M. Adductor Mandibularis Externus Profundus. (Fig. 10)

G. This muscle lies ventral to the adductor mandibularis externus medius, and dorsal to the adductor mandibularis posterior. It is separated anteriorly from the latter two muscles by a fascia. They interweave posteriorly. The muscle originates from the anterior and anterodorsal surfaces of the quadrate, and from the lateral surface of the prootic. Insertion is onto the bodenaponeurosis and also onto the medial base of the coronoid.

M. Adductor Mandibularis Externus Superficialis. (Figs. 6, 9, and 15)

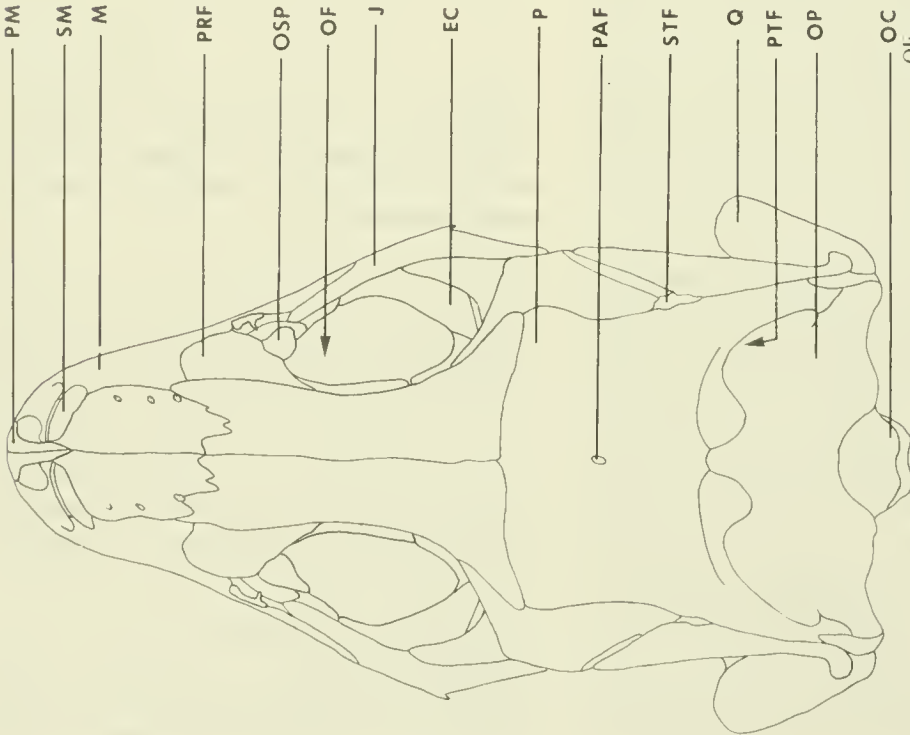
G. This thin superficial muscle is scarcely distinguishable from the deeper muscles. The muscle is separated by the bodenaponeurosis that extends from

B



PR Prootic
 PRF Prefrontal
 PT Pterygoid
 PTF Posttemporal Fenestra
 Q Quadrate
 S Squamosal
 SM Septomaxilla
 SO Supraoccipital
 ST Supratemporal
 STF Supratemporal Fontanelle

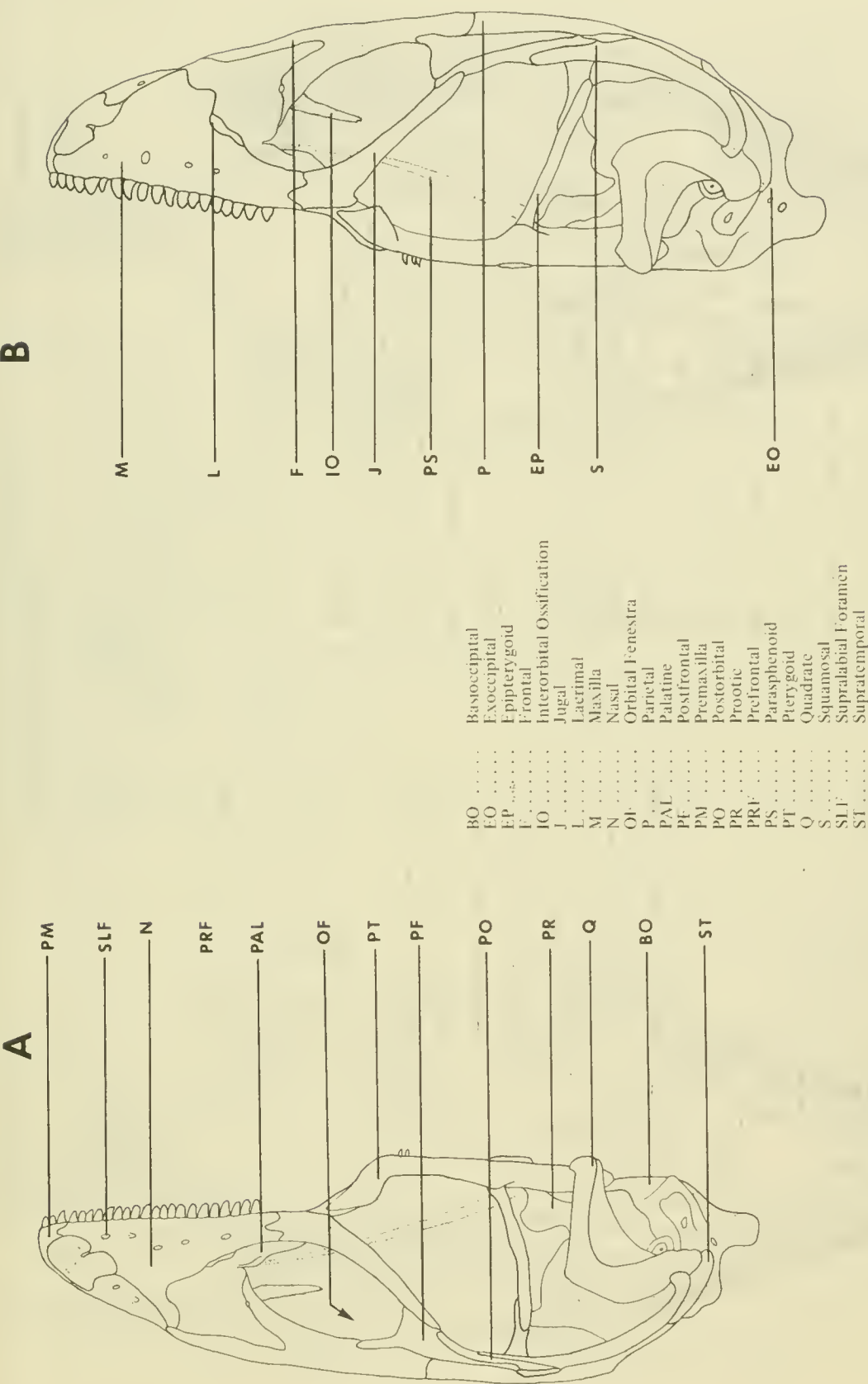
A



FC Ectopterygoid
 EN External Naris
 F Frontal
 IOF Infraorbital Fenestra
 J Jugal
 L Lacrimal
 M Maxilla
 N Nasal
 NF Nasal Foramen
 OC Occipital Condyle

A. *Eumeces gilberti* (9.2X) (SSC 303).
 B. *Eumeces gilberti* (9.3X) (BYU 31960).

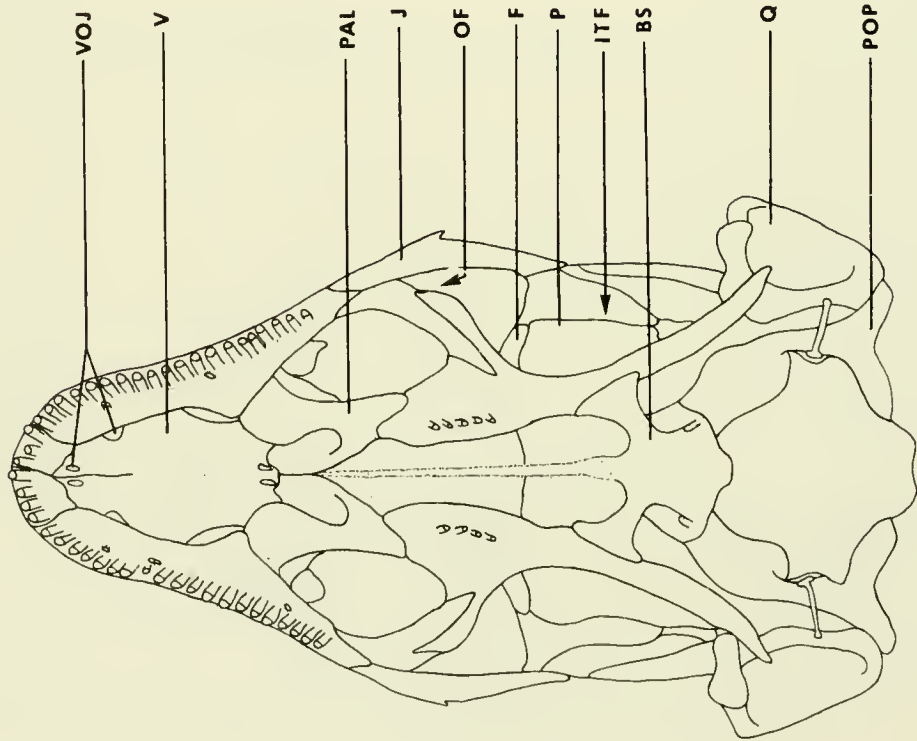
Figure 1. Dorsal view of skulls.



A. *Eunectes gilberti* (8.9X) (SSC 303)
B. *Eunectes skiltonianus* (9.3X) (BYU 31960)

Figure 2. Lateral view of skulls.

A

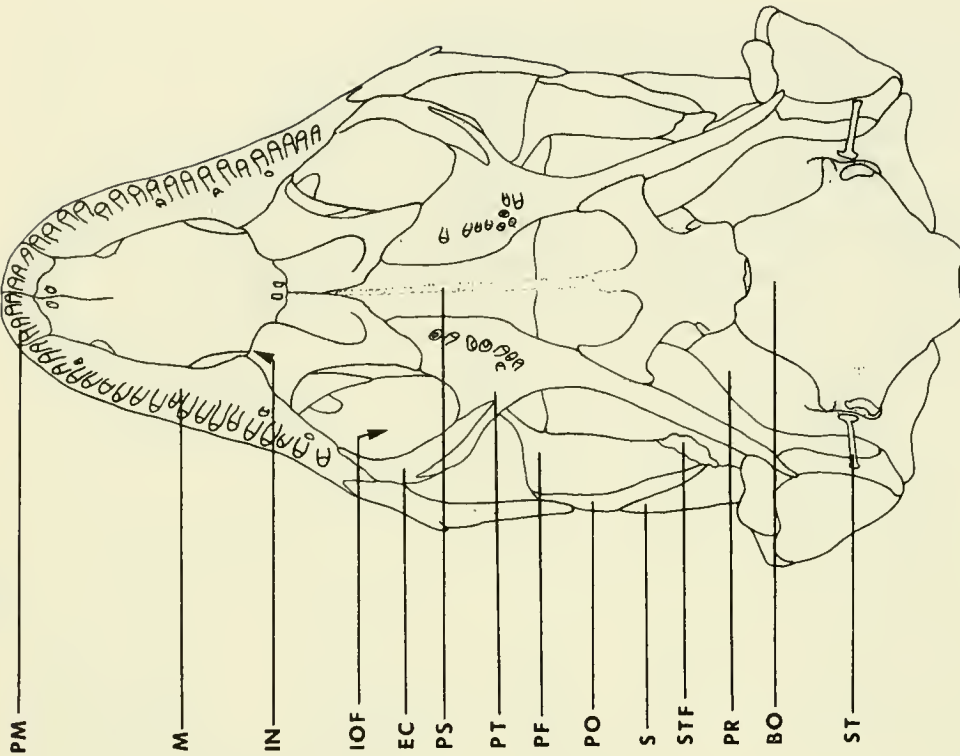


- | | |
|-----------|------------------------|
| BC | Basioccipital |
| BS | Basipterygoid |
| EC | Ectopterygoid |
| IN | Internal Naris |
| IOF | Infraorbital Fenestra |
| ITF | Infratemporal Fenestra |
| F | Frontal |
| J | Jugal |
| M | Maxilla |
| OF | Orbital Fenestra |

- | | |
|-----------|----------------------|
| P | Parietal |
| PAL | Palatine |
| PF | Postfrontal |
| PM | Premaxilla |
| PO | Postorbital |
| POP | Paroccipital Process |

A. *Eunectes gilberti* (9.2X) (SSC 303)
B. *Eunectes skiltonianus* (9.6X) (BYU 31961)

B



- | | |
|-----------|---------------------------------|
| PR | Prootic |
| PS | Parasphenoid |
| PT | Pterygoid |
| Q | Quadrate |
| S | Squamosal |
| STF | Supratemporal |
| STF | Supratemporal Fontanelle |
| V | Vomer |
| VOJ | Vomero-nasal Organs of Jacobson |

Figure 3. Ventral view of skulls.

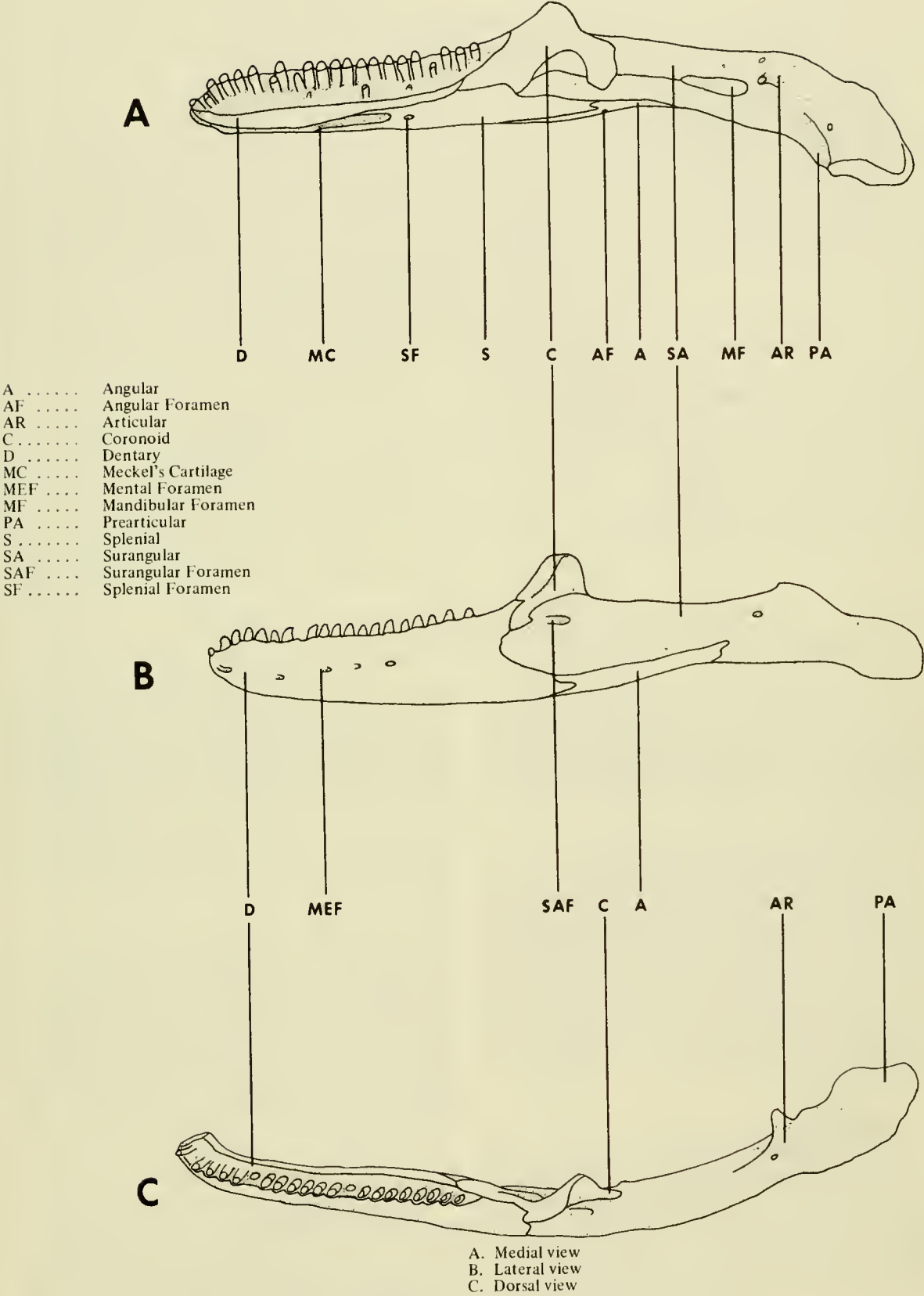


Figure 4. Mandible. *Eumeces skiltonianus* (9.3X) (BYU 12468)

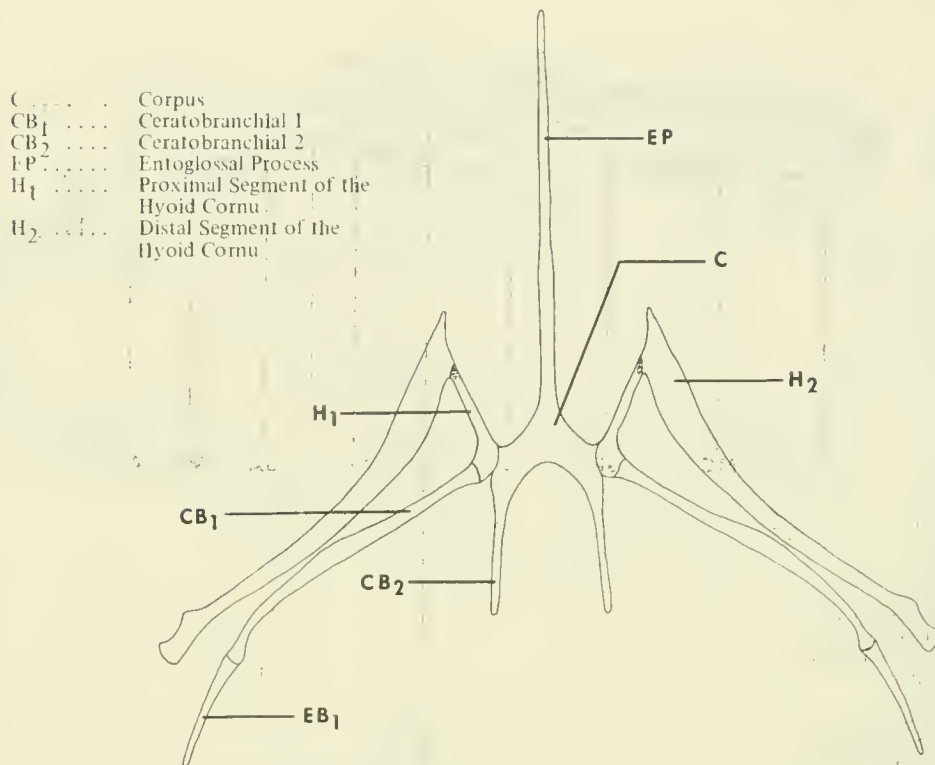


Figure 5. Dorsal view of hyoid apparatus. *Eunectes gilberti* (5.0X) (BYU 31956)

the coronoid and almost to the posterior margin of the muscle. It arises from the ventral surface of the squamosal, the dorsoanterior surface of the quadrate, and the anterior margin of the jugal. Insertion is into the bodenaponeurosis and on the lateral surface of the surangular.

M. Adductor Mandibularis Posterior. (Fig. 10)

G. This muscle is deep to the adductor mandibularis externis superficialis and ventral to the adductor mandibularis externis profundus. It is separated anteriorly from the latter muscle by a tendon; posteriorly the fibers of these two muscles interweave. Origin is on the anterior surface of the quadrate with insertion from the anterior surface of the quadrate with insertion on the medial dorsal surface of the surangular, the mandibular fossa, and the most anterior surface of the articular.

M. Anconaeus Coracoideus. (Fig. 6)

G. The anconaeus coracoideus is a small dorsal muscle arising by a tendon, posterior to the insertion of the latissimus dorsi, from the sternoscapular ligament and uniting with the anconaeus scapularis prior to insertion onto the olecranon process of the ulna. This muscle is found posterior to the anconaeus scapularis and anterodorsal to the anconaeus medialis humeralis.

M. Anconaeus Humeralis Lateralis. (Fig. 15)

G. This muscle originates medial to the insertion of the scapulodeltoideus and the clavodeltoideus from the proximal head and the anterior surface of the humerus. It then unites with the anconaeus scapularis to insert onto the olecranon process of the ulna. Some fibers will interdigitate distally with the brachialis inferior. This muscle is located anterior to the anconaeus scapularis and dorsal to the brachialis inferior.

M. Anconaeus Humeralis Medialis. (Fig. 6)

G. This muscle originates from the proximal end of the humerus, below the sternoscapular ligament, and from the posterodorsal surface of the shaft of the humerus. It then unites with the other anconaeus muscles for a common insertion onto the olecranon process of the ulna. This muscle lies posterior to the anconaeus coracoideus and anterior to the coracobrachialis longus.

M. Anconaeus Scapularis. (Figs. 6 and 15)

G. This large upper-arm muscle originates from the sternoscapular ligament dorsal to the scapulodeltoideus and clavodeltoideus. It then follows the humerus to join tendonously with the other anconaeus muscles. The muscle is divided into two bundles. The anterior bundle fibers extend first lateroven-

trally, then parallel to the humerus, and then ventromedially. This muscle is posterodorsal to the anconaeus humeralis lateralis and anterior to the anconaeus coracoideus.

M. Biceps. (Figs. 15 and 17)

G. The biceps is a large ventral muscle that inserts tendonously onto the proximal head of the ulna and radius. The muscle continues along the humerus and forms a broad tendon which is connected to the head of this muscle. The origin is from the medial ventral border of the scapula. On the humerus the muscle lies between the brachialis inferior and the coracobrachialis longus. Just lateral to the deltopectoral process an anterior slip is attached tendonously to this process. On the scapula a thin layer of the supracoracoideus covers the anterior portion of this muscle.

M. Brachialis Inferior. (Fig. 17)

G. This ventral muscle originates from the antero-lateral surface of the deltopectoral process and the anteroventral surface of the shaft of the humerus. Insertion is primarily onto the radius; however, some fibers interdigitate distally with the biceps to also insert onto the ulna. This muscle is located anterior to the biceps and posterior to the anconaeus humeralis lateralis.

M. Branchiohyoideus. (Fig. 17)

G. This straplike muscle originates from the lateral three-fourths of the ceratobranchial 1 and inserts onto the posterior and ventral surfaces of the central portion of the hyoid cornu. This muscle is superficial to the sternocleidomastoideus and trapezius laterally, and is strongly attached to these two muscles by connective tissue.

M. Clavodeltoideus. (Figs. 6, 9, 12, 13, 15, 16, and 17)

G. This complex muscle inserts by a tendon onto the deltopectoral process near the origin of the brachialis inferior and the insertion of the scapulodeltoideus. Some of the fibers interdigitate with the scapulodeltoideus prior to insertion. From the insertion the muscle fibers extend in two directions to originate from the clavicle. One bundle of fibers extends anteromedially under the clavicle bar, rotates ventrally and laterally to originate from the medioventral surface of the clavicle. The other bundle of fibers extends anteromedially under the clavicle-interclavicle bar to originate from the dorsomedial surface of the clavicle.

M. Constrictor Colli. (Figs. 6, 9, and 15)

G. This is a wide cervical muscle originating from the middorsal fascia and the tympanic fascia. Insertion is with its partner in the median fascia. This muscle is strongly attached laterally and ventrally by

fascia to the trapezius, the sternocleidomastoideus, and the pectoralis. In some specimens fat tissue is found in abundance on the ventral and lateral surfaces.

M. Coracobrachialis Brevis. (Fig. 17)

G. This posterior arm muscle originates from the medioventral surface of the scapula with the fibers converging laterally to insert onto the deltopectoral process and onto almost the entire length of the posteroventral surface of the humerus. This muscle is located anterior to the coracobrachialis longus and is deep to the biceps.

M. Coracobrachialis Longus. (Figs. 6 and 15)

G. This muscle has a dorsal and a ventral slip which have a common insertion onto the ulnar process of the humerus. The ventral slip is considerably larger and originates from the posterolateroventral tip of the scapula. The dorsal slip originates from the dorsal surface of the scapula just posterior to the origin of the subscapularis 2. It leaves the scapula dorsal to the origin of the ventral slip and shortly terminates in a long slender tendon to insert onto the ulnar process.

M. Costocoracoideus. (Not figured)

G. This broad, thin muscle originates from the first sternal rib and extends anteriorly to insert onto the sternum and the sternoscapular ligament.

M. Depressor Mandibularis. (Figs. 6, 9, and 15)

G. This muscle originates from the middorsal fascia, the posterodorsal surface of the squamosal, and the most lateral surface of the parietal. The anterior muscle fibers converge centrally, attach to the posterodorsal edge of the quadrate, the posterior margin of the tympanic fascia and then insert onto the retroarticular process by a wide tendon. The more posterior fibers converge anteroventrally to insert lateroventrally onto the superficial fascia of the intermandibularis posterior. This muscle is not easily distinguishable nor easily separable into anterior and posterior bundles. It is deep to the constrictor colli and superficial to the geniohyoideus, the sternocleidomastoideus, the trapezius, and the most posterior edge of the adductor mandibularis externus superficialis.

S. This muscle is easily separable into anterior and posterior bundles. The anterior bundle is small and originates from the posterodorsal surface of the squamosal. It terminates in a wide tendon, and then joins with the posterior bundle to insert onto the retroarticular process. It is deep to the posterior bundle and superficial to the sternocleidomastoideus. The posterior fibers of the posterior bundle originate and insert similarly to *gilberti*.

M. External Sternocoracoideus. (Not figured)

G. The external sternocoracoideus originates from the anterolateral border of the sternum with fibers extending anteriorly to fuse with the internal sternocoracoideus for a tendonous insertion onto the scapula, medial to the origin of the subscapularis muscles.

M. Genioglossus. (Figs. 10 and 15)

G. The genioglossus originates from the anteromedial one-fifth of the mandible and inserts posteriorly by medial and lateral slips onto the hyoglossus and tongue fascia. It is strongly attached dorsally to the oral membrane. There is a small slip of this muscle which attaches anteromedially to the skin fascia. The muscle is lateral to the entoglossal process and the trachea, and medial to the mandibulo-hyoideus 1.

M. Geniohyoideus. (Fig. 15)

G. The origin of the geniohyoideus is along the anterior margin of the ceratobranchial 1 and the posteroventral one-third of the entoglossal process of the hyoid apparatus. The muscle fibers continue anterolaterally, interdigitate with six or seven slips from the intermandibularis anterior, and insert along the medial surfaces of the dentary and angular. It is deep to the intermandibularis anterior, the constrictor colli, and the depressor mandibularis. The body of the muscle is superficial to the pterygomandibularis, the mandibulo-hyoideus 1, the hyoglossus, the genioglossus, and the trachea.

S. The only difference noted is that this muscle is interdigitated with five to seven slips from the intermandibularis anterior. (See M. Intermandibularis Anterior)

M. Hyoglossus. (Fig. 16)

G. The hyoglossus is a thin sheet muscle that originates from the anterior side of the ceratobranchial 1 and inserts anteriorly with the tongue fascia and with interdigitation by medial and lateral slips of the genioglossus. This muscle is deep to the geniohyoideus and superficial to the oral membrane, the mandibulo-hyoideus 1, and portions of the hyoid apparatus, the branchiohyoideus, and the pterygiomandibularis.

M. Intercostalis Externis. (Fig. 14)

G. This muscle originates from the posterolateral edge of the ribs and inserts onto the anterolateral edge of the following posterior rib. This muscle is deep to the obliquus abdominus profundus and to the sacrolumbalis and superficial to the intercostalis internis. It does not cover the intercostalis internis ventrally and the muscle become thicker dorsally. Dorsally and anteriorly, fibers of this muscle join with those of the sacrolumbalis and obliquus abdo-

minus profundus to insert onto the ventrolateral surface of the axis.

M. Intercostalis Internis. (Figs. 14 and 17)

G. The fibers of this muscle originate from the ribs and insert onto the following posterior rib. On the ventral surface the muscle is nearly parallel to the bilateral axis of the body, and as it extends dorsally the fibers change to a vertical and slightly posterior direction. It is deep to the intercostalis externis and superficial to the obliquus abdominus internis.

M. Intermandibularis Anterior. (Fig. 15)

G. This ventral muscle originates from the medial surface of the mandible and inserts with the opposite muscle in the median fascia. Posteriorly the muscle becomes thinner and is continuous with the mandibularis posterior. This muscle is divided into six or seven medially fused slips which are irregular in size and which interdigitate with the geniohyoideus. In the specimens studied the number of slips was approximately equally divided between six and seven.

S. This muscle is subdivided into five to seven medially fused slips which are irregular in size and which interdigitate with the geniohyoideus. A sub-specific difference is observed. The number of slips in *skiltonianus* ranges from five to six; whereas, in *utahensis* the number of slips ranges from six to seven.

M. Intermandibularis Posterior. (Figs. 9 and 15)

G. This thin sheet muscle originates ventral to the adductor mandibularis externis superficialis by fascia from the ventrolateral surface of the angular and the prearticular, and also from the fascia covering the quadrate. Insertion is ventrally with its partner in the median fascia. The muscle begins just posterior to the last slip of the intermandibularis anterior and terminates slightly posterior to the tympanic cavity. It is deep to the depressor mandibularis posteriorly. This muscle is superficial to the anterolateral portion of the pterygomandibularis.

M. Internal Sternocoracoideus. (Not figured)

G. This thin rectangular muscle arises from the posterolaterodorsal surface of the sternum and unites anteriorly with the external sternocoracoideus for a common tendonous insertion onto the scapula, medial to the origin of the subscapularis muscles.

M. Latissimus Dorsi. (Figs. 6, 7, 9, and 15)

G. The fibers of the latissimus dorsi originate from the ligamentum nuchae, converge ventrally, and pass most medially between the anconaeus coracoideus and anconaeus scapularis to insert tendonously onto the shaft of the humerus. These muscle fibers are deep to the skin and are superficial to the posterior portion of the scapulodeltoideus.

M. Levator Pterygoideus. (Fig. 12)

G. This muscle is deep to the pseudotemporalis profundus. It originates from the lateral surfaces of the prootic and parietal descending processes. Fibers extend ventrally to insert onto the lateral and medial surfaces of the pterygoid, just posterior to the fossa columella.

M. Levator Scapulae Profundus. (Figs. 12 and 16)

G. This narrow somewhat triangular muscle originates in common with the levator scapulae superficialis from the atlas and inserts posteriorly onto the clavicle bar, ventral to the levator scapulae superficialis. It is superficial to the esophageal membrane and deep to the trapezius.

M. Levator Scapulae Superficialis. (Figs. 7 and 12).

G. This muscle arises from the atlas with the levator scapulae profundus and inserts onto the anterolateral surface of the suprascapula. This muscle is thick anteriorly but becomes thinner and fan-shaped posteriorly. It is deep to the lateral trunk muscles and is lateral to the rectus capitis anterior.

M. Longissimus Cervicis. (Figs. 8, 12, 13, and 17)

G. This muscle is located ventral to the obliquus capitis magnus. Its origin is by fusion with the myosepta between the obliquus capitis magnus and the lateral bundle of the spinalis capitis. The fibers extend in a ventroanterior direction to insert tendonously onto the basioccipital process.

M. Mandibulohyoideus 1. (Fig. 16)

G. The origin of this muscle is from the ventromedial surface of the dentary and the angular, and inserts onto the most anteroventral surface of the distal segment of the hyoid cornu. One to two slips of the intermandibularis anterior interdigitate with this muscle. It is superficial to the oral membrane and the medial portion of the pterygomandibularis, and lies lateral to the geniohyoideus.

M. Obliquus Abdominus Externis. (Figs. 6, 9, and 15)

G. This sheet muscle originates anterolaterally from the ribs of the sixth and seventh vertebrae and laterally from the sacrolumbalis. Insertion is with the pectoralis and rectus abdominus ventrolaterally.

M. Obliquus Abdominus Internis. (Fig. 14)

G. This thin, loosely arranged sheet muscle originates from the inner surface of the ribs and inserts anteriorly onto the esophageal membrane, the sternum, and the ventral heads of the thoracolumbar ribs. The fibers are superficial to the transversalis and deep to the intercostalis internis. They extend in a dorsal and slightly posterior direction.

M. Obliquus Abdominus Profundus. (Figs. 13 and 17)

G. This muscle has the same origin as the externis

muscle except that some fibers will continue anterodorsally and become almost parallel with the sacrolumbalis to interdigitate with that muscle and the intercostalis externis to insert onto the axis. Insertion is also by individual slips onto the sternal ribs with the most lateral fibers being attached to the most posterior rib. This muscle is generally heavier than the externis muscle.

M. Obliquus Capitis Magnus. (Figs. 8, 12, and 13)

G. This muscle originates from a myosepta with the lateral slip of the spinalis capitis. The myosepta extends lateroventrally from the fifth vertebrae to the atlas. Insertion is onto the supratemporal, the paroccipital process, and the parietal.

M. Pectoralis. (Figs. 15 and 16)

G. The pectoralis is a thick muscle having its origin from the lateral process of the interclavicle, the sternum, the mesosternum and the ribs which are attached to the mesosternum, and the first two thoracolumbar ribs. Its origin along the ribs is in a steplike fashion laterally, with the most lateral slip fusing with the rectus abdominus. All fibers converge to insert tendonously onto the deltopectoral process of the humerus. This muscle is deep to the skin and to a lateral slip of the rectus abdominus. It overlies a broad ligament from the interclavicle lateral process to the sternum and the posterior portion of the scapula with its attached muscles.

M. Protractor Pterygoideus. (Fig. 12)

G. The anterior portion of this muscle is deep to the pseudotemporalis profundus. Origin is from the anterolateral surface of the prootic. Fibers extend lateroventrally and posteriorly to insert onto the pterygoid and the quadrate process of the pterygoid.

M. Pseudotemporalis Profundus. (Fig. 11)

G. This muscle is deep to the adductor mandibularis externis profundus and the adductor mandibularis externis medius. It originates from the descending processes of the prootic and the parietal; and also from the lateral, posterior and anterior surfaces of the epipterygoid. Some of the dorsal fibers originate from the ventral surface of the parietal. The muscle continues in a nearly anteroventral direction to insert onto the base of the coronoid and posteriorly onto the surangular and the mandibular fossa.

M. Pseudotemporalis Superficialis. (Fig. 11)

G. This muscle is located medial to the adductor mandibularis externis medius and dorsolateral to the adductor mandibularis externis profundus. Origin is from the ventral surface of the parietal medial to the supratemporal fontanelle. Fibers extend ventrally to insert tendonously onto the dorsal surface of the coronoid.

M. Pterygomandibularis. (Figs. 7, 10, 13, 15 and 17)

G. The pterygomandibularis originates tendonously from the pterygoid and the epipterygoid. The muscle continues posteriorly along the pterygoid, attaches to the pterygoid, the basiptyergoid process, and then covers the ventrolateral surfaces of the angular, the articular, the medial surface of the surangular, and the medial dorsal surface of the retroarticular process. The muscle then extends dorsally around the posterior end of the retroarticular process to insert onto the condyle of the quadrate and the angular process of the articular. It is deep to all ventral and lateral muscles and is covered by an extensive fascia.

M. Rectus Capitis Anterior. (Figs. 14 and 17)

G. This is a thick straplike muscle originating by two slips from the ventral surface of the eighth and seventh vertebrae and their rib capitulae. Anteriorly the two slips fuse. The combined muscle interdigitates with its opposite partner and secondarily arises from the ventral spinous processes of the remaining anterior vertebrae. Insertion is medial to the longissimus cervicis onto the basioccipital and its process. The body of the muscle lies dorsal to the esophagus and ventral to the longissimus cervicis.

M. Rectus Capitis Posterior. (Figs. 8, 13, and 17)

G. Anteriorly this muscle is deep to the spinalis capitis and medial to the obliquus capitis magnus. In the vicinity of the seventh vertebrae the muscle is deep only to the dorsal fascia, is medial to the lateral portion of the spinalis capitis, and lateral to the ligamentum nuchae. It is separated into anterior and posterior bundles by a myosepta with some interdigitation in the vicinity of the fourth vertebrae. The anterior bundle is divided into a lateral and a medial slip which are interdigitated but separable. The lateral slip makes the myosepta connection with the posterior bundle and originates from the second, third, and fourth vertebrae with insertion onto the paroccipital process, the parietal, and the supratemporal. The medial slip originates from the atlas and inserts onto the prootic and the supraoccipital elements. The most anterior portion of the posterior bundle lies deep to the anterior bundle and inserts tendonously onto the axis.

M. Sacrolumbalis. (Figs. 6 and 9)

G. This superficial epaxial muscle originates from the crest of the ilium and inserts tendonously onto the ribs. Anteriorly, fibers of this muscle will join those of the intercostalis externis and the obliquus abdominus profundus to insert onto the ventrolateral process of the axis. This muscle interdigitates laterally with the obliquus abdominus muscles. This muscle is superficial to the intercostalis externis dorsally.

M. Scapulodeltoideus. (Figs. 6, 9, 12, and 13)

G. This triangular shaped muscle originates primarily from the lateral surface of the suprascapula with some fibers originating from the clavicle bar. Insertion is tendonously onto the deltopectoral process of the humerus. The muscle is ventral to the levator scapulae muscles and superficial to the scapulohumeralis muscles.

M. Scapulohumeralis Anterior. (Figs. 14 and 17)

G. This muscle has two slips. The dorsal slip inserts onto the anterior edge of the humerus next to the glenoid fossa beneath the sternoscapular ligament. The fibers continue anterodorsally to originate from the most dorsoanterior surface of the scapular bar and the most anteroventral surface of the suprascapula. The second slip, which is the longer, has the same origin but inserts onto the ventrolateral border of the scapula. Centrally the two slips are joined by a myosepta.

M. Scapulohumeralis Posterior. (Figs. 8, 14, and 17)

G. This rectangular shaped muscle inserts onto the proximal end of the humerus next to the glenoid fossa, posterior to the insertion of the scapulohumeralis anterior and medial to the insertion of the latissimus dorsi. The fibers continue anterodorsally covering some of the fibers of the serratus ventralis to originate from the posterolateral surface of the suprascapula and the scapular bar.

M. Serratus Dorsalis. (Fig. 8)

G. This muscle arises from the lateral surface of the first three cervical ribs by three slips and inserts onto the dorsal surface of the suprascapula. They slightly overlap one another by the posterior succeeding one.

M. Serratus Ventralis. (Figs. 8 and 13)

G. This is a wide straplike muscle which originates from the ribs of the sixth and seventh vertebrae, dorsal to the origin of the obliquus abdominus muscles. Insertion is onto the posteromedial border of the suprascapula and the dorsolateral portion of the scapular bar. This muscle is deep to the latissimus dorsi and the trapezius.

M. Spinalis Capitis. (Figs. 7, 8, 12, and 13)

G. This muscle originates along the cervical and thoracicolumbar vertebrae and inserts along the entire posterior portion of the parietal. Anteromedially, fibers insert tendonously onto the side of the supraoccipital ridge. The muscle has a medial and a lateral portion which are unseparable. The medial portion is superficial to the rectus capitis posterior and thins posteriorly to terminate near the seventh vertebrae. The lateral portion participates in a myosepta with some of the deeper muscles and continues poster-

iorly, lateral to the rectus capitis posterior.

M. Subscapularis 1. (Not figured)

G. This muscle has three slips which converge posteriorly to insert by a common tendon onto the humeral head. The most anterior slip originates from the anterodorsal border of the scapula. The most lateral slip of the two posterior slips originates from the scapular bar and the suprascapula; whereas, the medial slip originates from the scapular bar. They both converge posteriorly to join the anterior slip.

M. Subscapularis 2. (Not figured)

G. The fibers of this muscle originate from the majority of the dorsal surface of the scapula and converge to insert onto the humeral head dorsal to the insertion of the subscapularis 1. This muscle is located between the anterior slip of the subscapularis 1 and the dorsal slip of the coracobrachialis longus, and lies lateral to the origin of the internal sternocoracoideus.

M. Supracoracoideus. (Fig. 17)

G. This ventral muscle has a wide origin from the anteromedial surface of the scapula with the fibers converging to insert tendonously onto the medial surface of the deltopectoral crest of the humerus. This muscle is located posterior to the clavodeltoideus and anterior to the biceps. On the scapula a thin layer of fibers will cover the anteroventral surface of the biceps. It is thicker anteriorly.

M. Sternocleidomastoideus. (Figs. 6, 9, 11, and 15)

G. This wide, thick ribbonlike muscle originates from the posterior surfaces of the parietal, the squamosal, and the quadrate. It extends ventroposteriorly to insert onto the lateral process of the interclavicle. Near its insertion this muscle is fused with the trapezius. It is deep to the depressor mandibularis, the ceratobranchial 1, the branchiohyoideus, and the lateral portion of the trapezius. It is superficial to the neck muscles and to the insertion of the trapezius and the sternohyoideus.

M. Sternohyoideus. (Figs. 10, 12, 15, and 16)

G. The sternohyoideus is a thick sheet muscle having a superficial and a profundus layer. Some of the fibers slightly intermix medially and tend to become parallel to the bilateral axis; however, the muscle is easily separable into two layers. The ventral layer is slightly larger and originates from the posterior and ventral surfaces of the ceratobranchial 1 and medially from the corpus. Its fibers extend posterolaterally to insert onto the lateral process of the interclavicle and the clavicle-suprascapular bar,

adjacent to the attachment of the trapezius. At its insertion this muscle joins with the sternocleidomastoideus and the trapezius. It is deep to portions of the sternocleidomastoideus, trapezius, depressor mandibularis, and the constrictor colli. The dorsal layer extends further laterally than the superficial layer and has its origin from the posterior surface of the ceratobranchial 1 and 2. Fibers continue posteromedially to insert onto the lateral process of the interclavicle. This layer is superficial to the pharyngeal membrane, the thyroid gland, and portions of the clavodeltoideus and the scapulodeltoideus. Medially, this muscle borders an elliptical space as previously mentioned in the section, General Description of the Myology.

M. Transversalis. (Fig. 14)

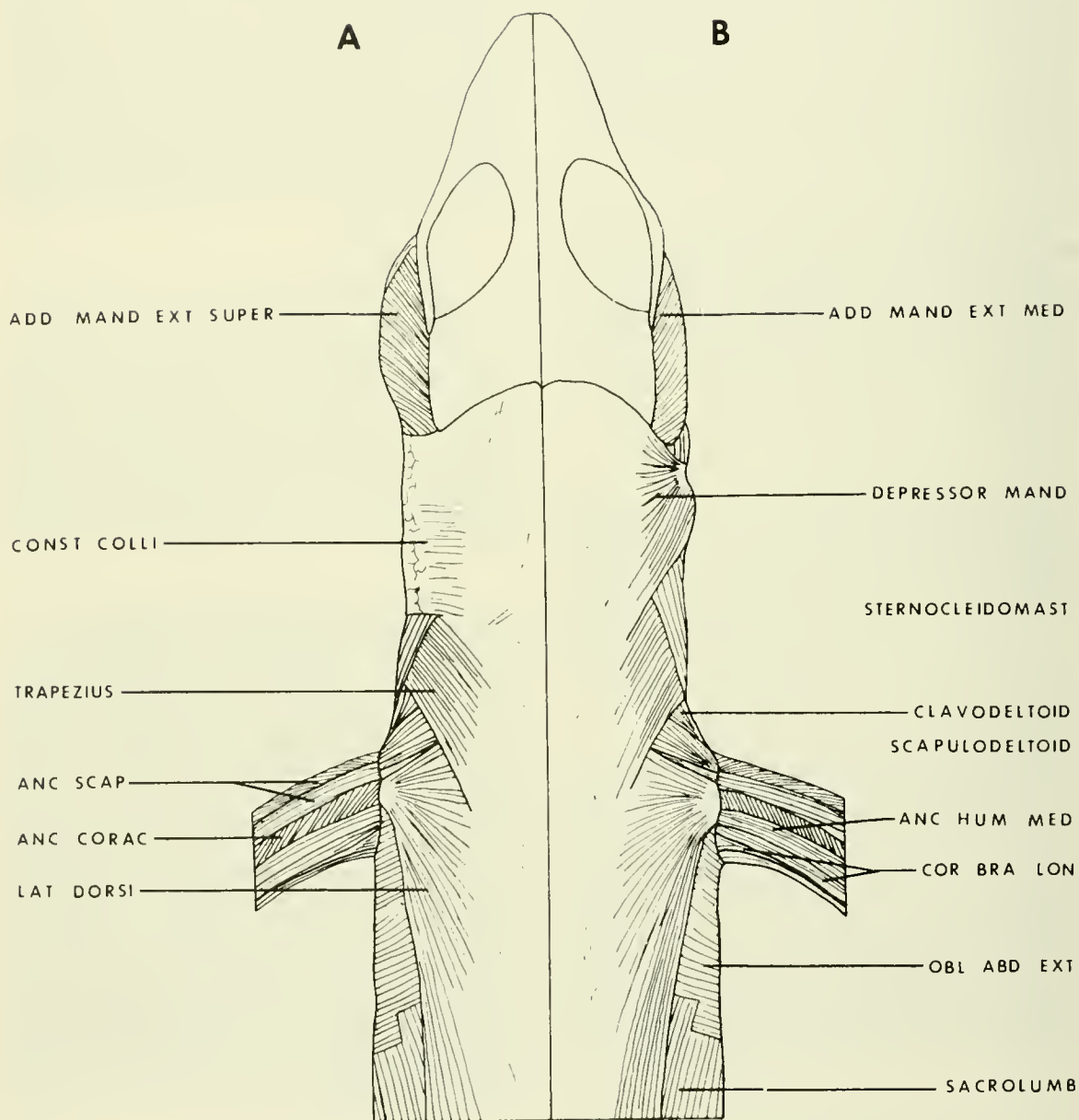
G. This loosely arranged muscle arises from a fascia which extends from the pelvis to the neck region and inserts ventrally onto the ribs, the lateral surface of the sternum, and the dorsal surface of the rectus abdominus. The fibers extend in a dorsoanterior direction, are superficial to the peritoneal membrane and are deep to the obliquus abdominus internis.

M. Trapezius. (Figs. 6, 7, 9, 11, 15, and 16)

G. The trapezius originates from the middorsal fascia and covers a majority of the lateral musculature. It narrows laterally to insert ventrally onto the clavicle bar and the lateral process of the interclavicle which in turn is attached to the sternum by a broad ligament. On the ventral surface the muscle fuses with the sternocleidomastoideus. In some specimens this muscle is attached to the pectoralis by a tendinous fascia. The trapezius is variable in thickness with the anterior fibers usually being thicker. Toward the center they become thinner and in some specimens can be separated into two bundles. In this case the anterior bundle inserts onto the lateral process of the interclavicle and the most ventral portion of the interclavicle-clavicle bar. The posterior bundle inserts onto the posterior border of the clavicle bar, dorsal to the sternocleidomastoideus.

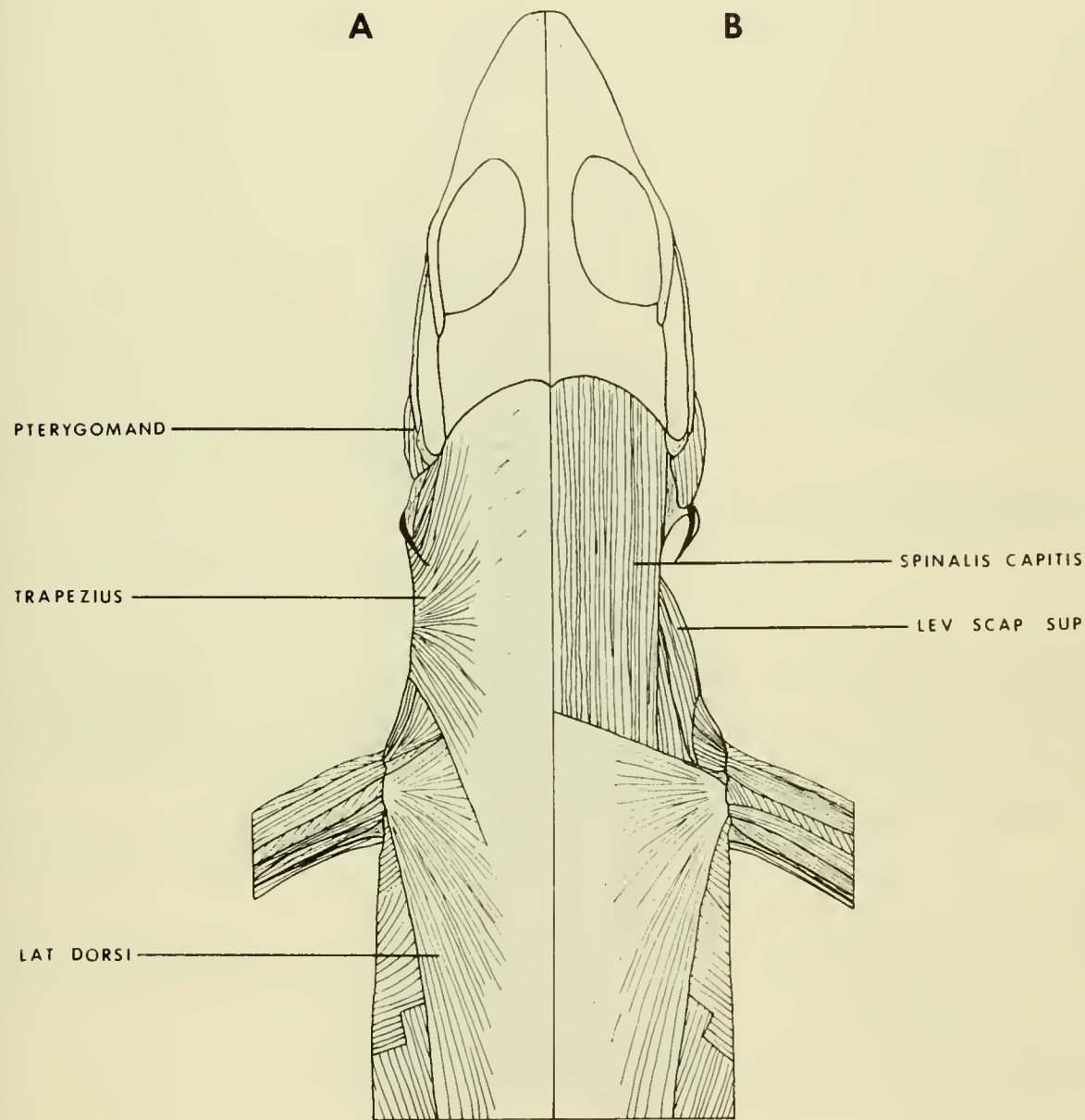
Unnamed Muscle. (Not figured)

The following muscle was found in *E. gilberti* (BYU 31956). It is a thin horizontal straplike muscle originating by fascia from the ribs of the twelfth and thirteenth vertebrae and inserting onto the anterior edge of the insertion of the serratus ventralis, and also onto the suprascapula. This muscle is deep to the latissimus dorsi. It was not present in any other specimen of *gilberti* or *skiltonianus* studied.



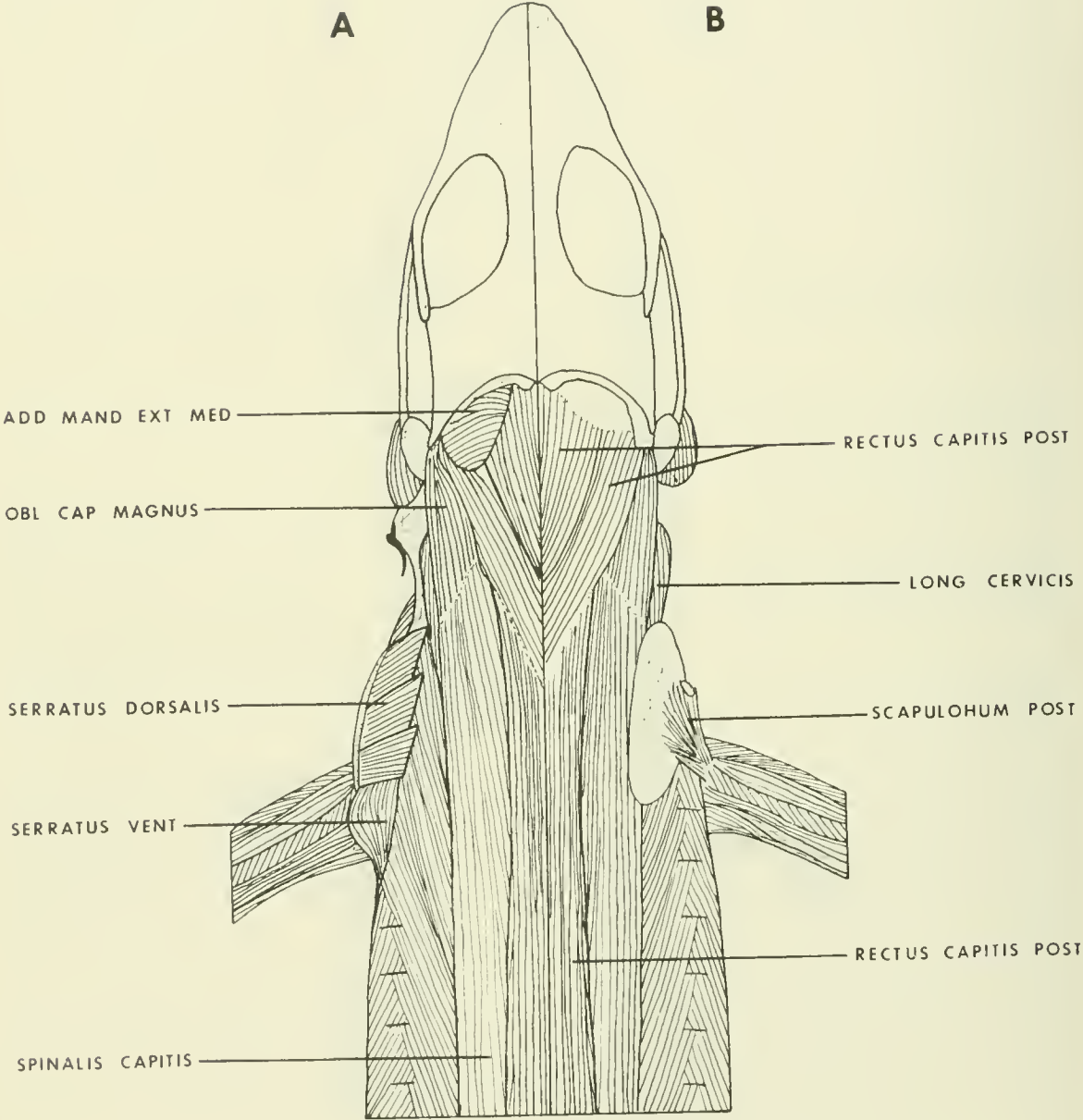
A. Superficial depth
B. First depth

Figure 6. Musculature dorsal view. *Eumeces gilberti* (3.7X) (BYU 31956).



A. Second depth
B. Third depth

Figure 7. Musculature dorsal view, *Eumeces gilberti* (3.7X) (BYU 31956).



A. Fourth depth
B. Fifth depth

Figure 8. Musculature dorsal view, *Eumeces gilberti* (3.7X) (BYU 31956).

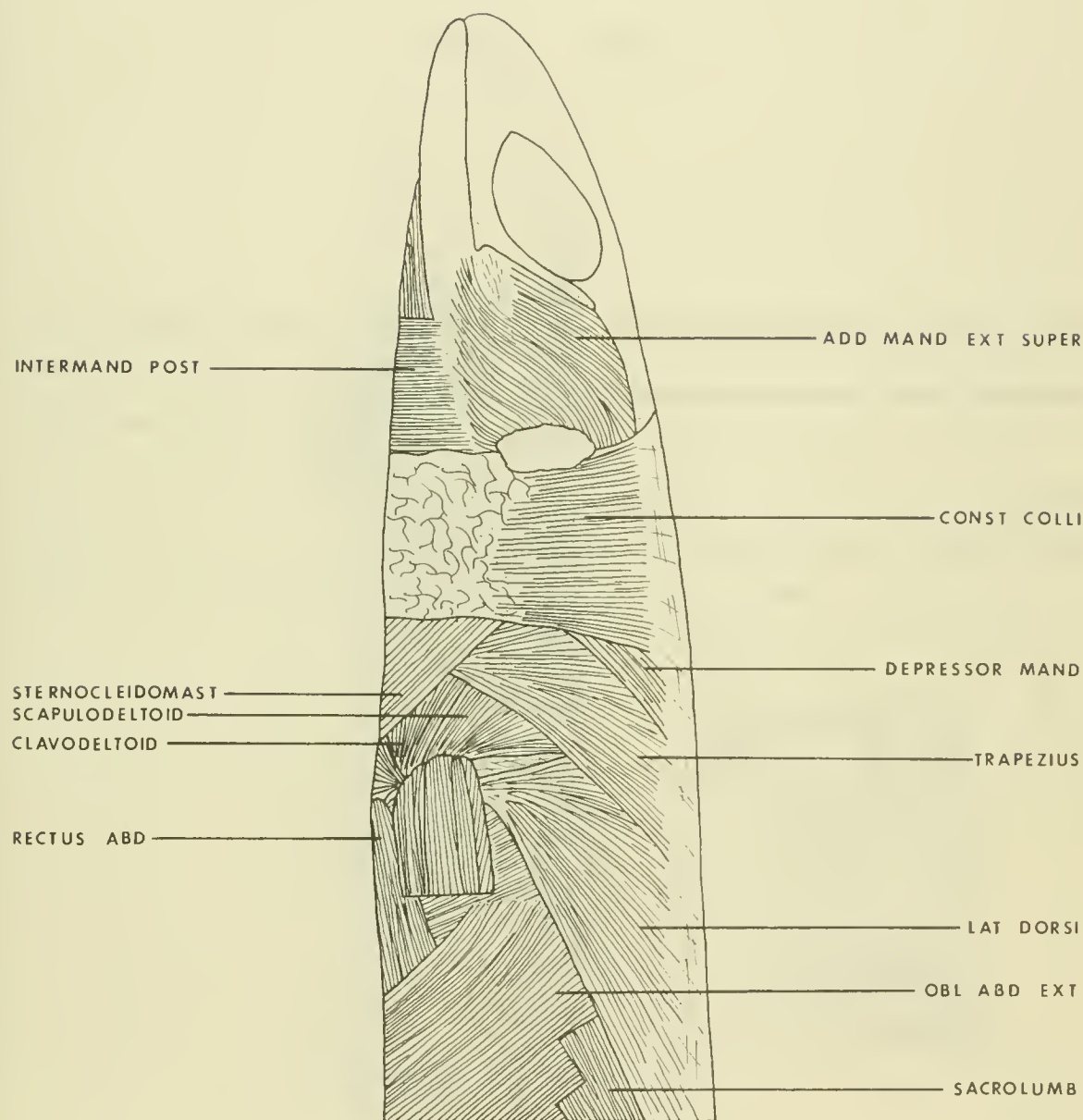


Figure 9. Musculature lateral view. Superficial depth. *Eumeces gilberti* (3.7X) (BYU 31956).

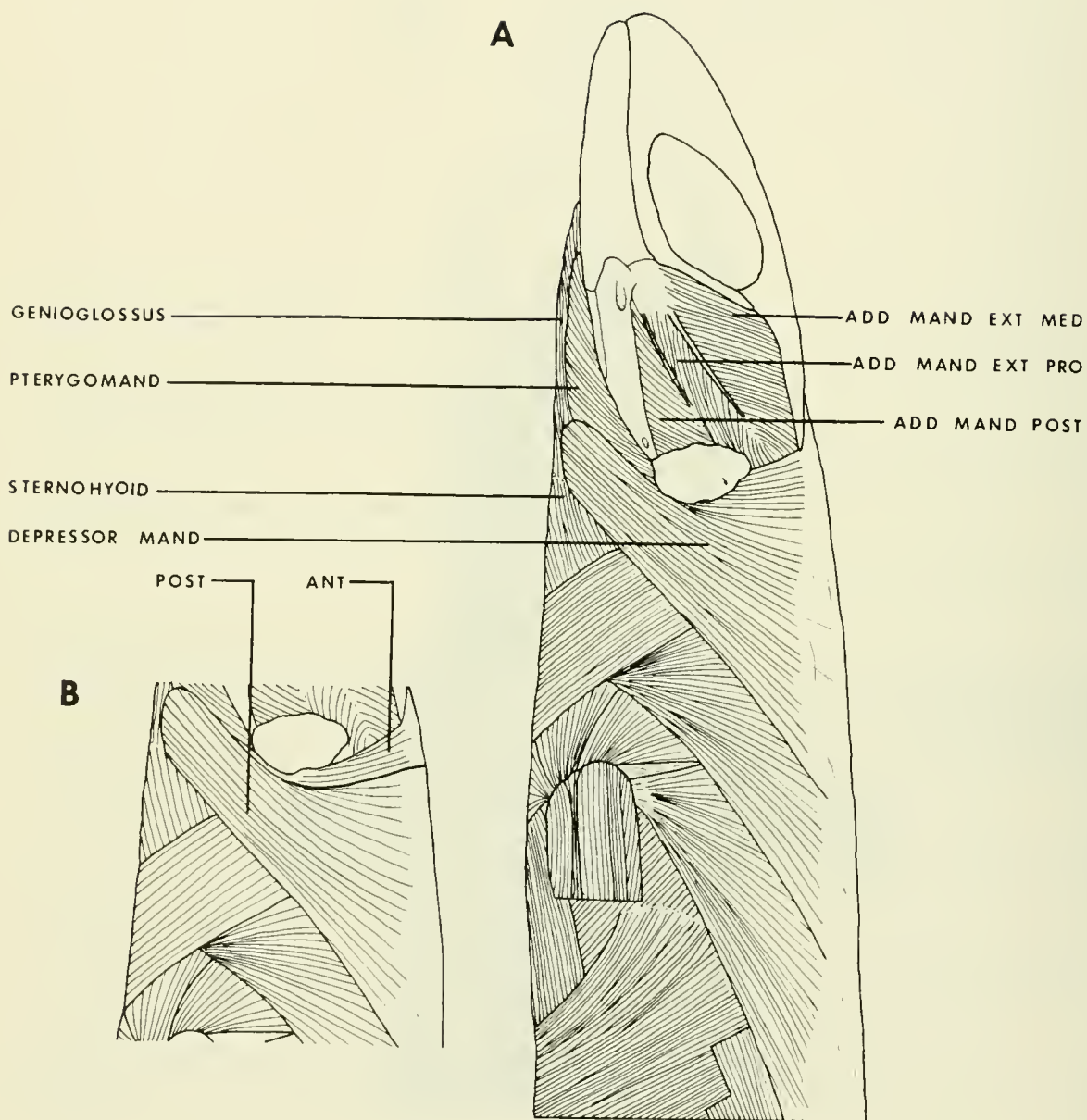


Figure 10. Musculature lateral view, First depth. A. *Eumeces gilberti* (3.7X) (BYU 31956). B. *Eumeces skiltonianus* (5.7X) (BYU 12474). Showing anterior and posterior bundles of the depressor mandibularis.

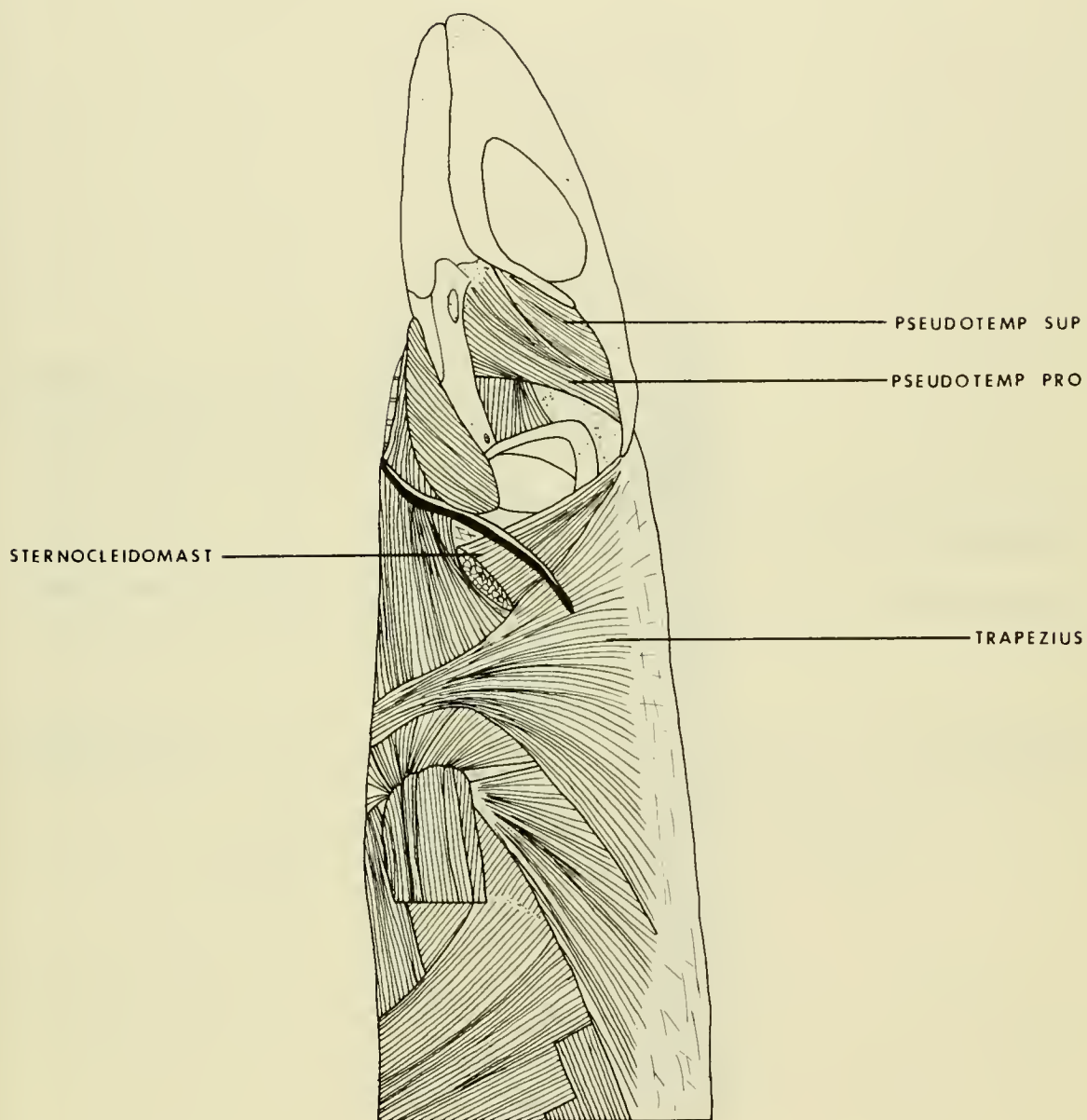


Figure 11. Musculature lateral view. Second depth. *Eumeces gilberti* (3.7X) (BYU 31956).

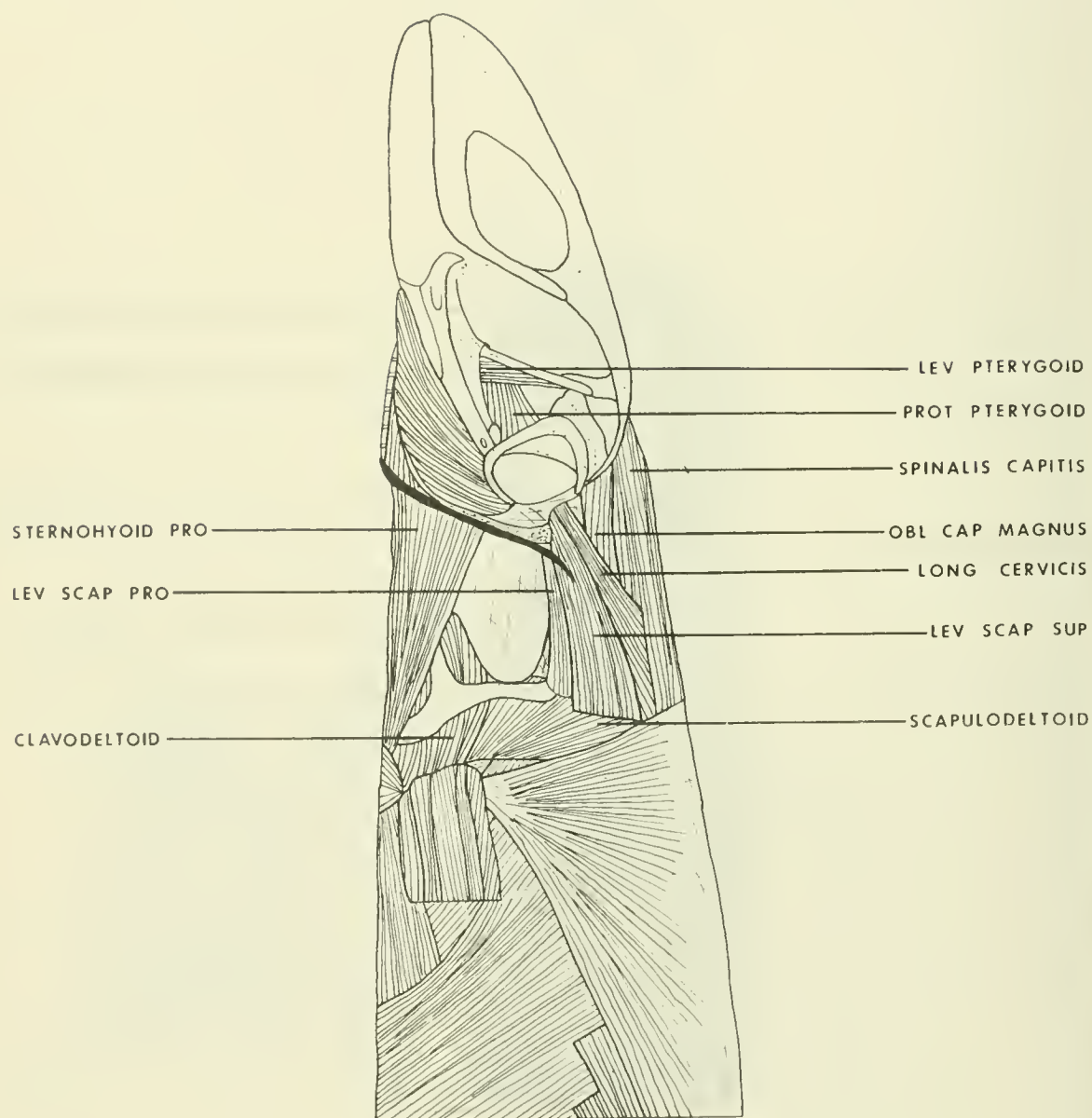


Figure 12. Musculature lateral depth. Third depth. *Eumeces gilberti* (3.7X) (BYU 31956).

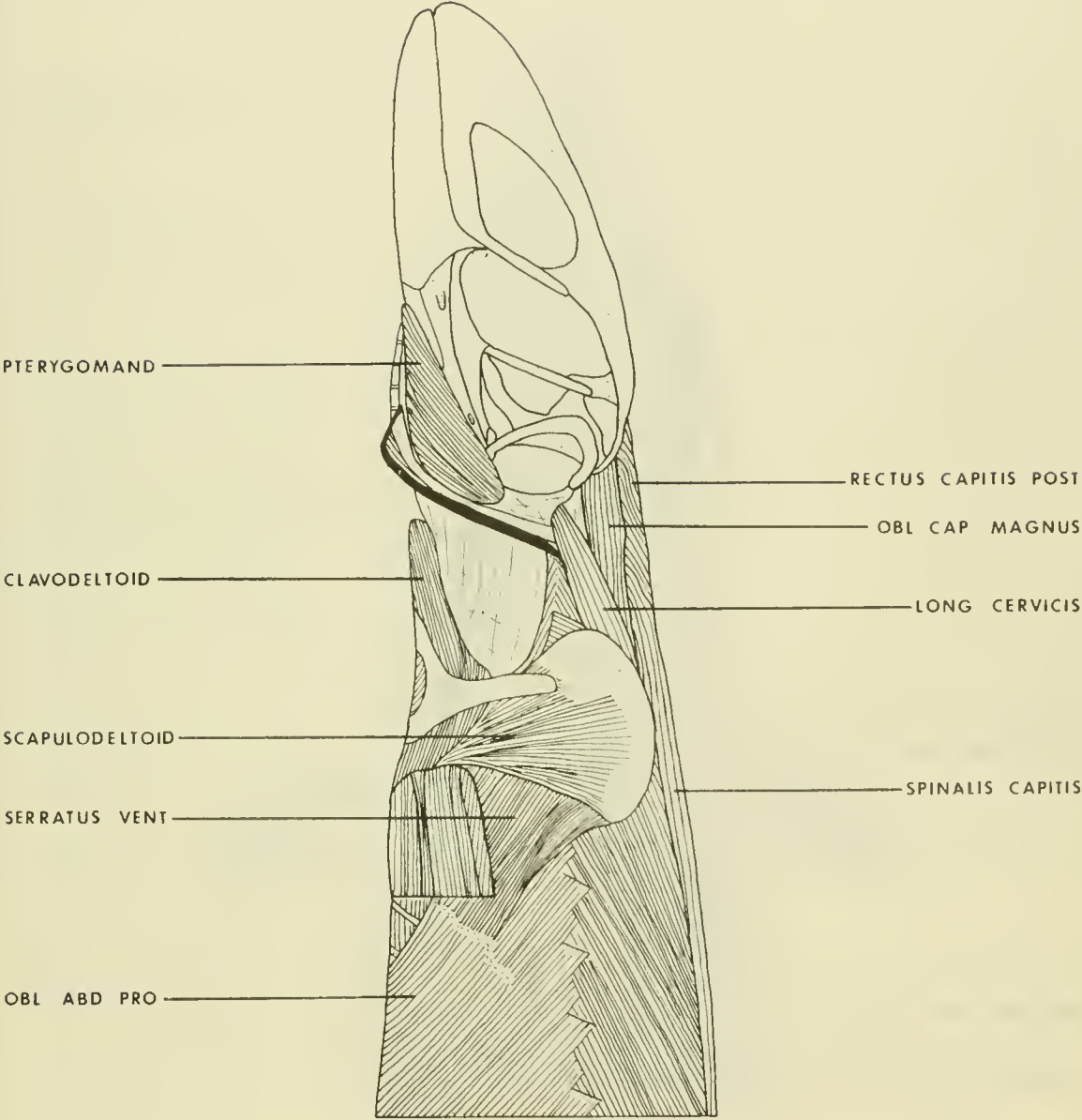


Figure 13. Musculature lateral depth. Fourth depth, *Eumeces gilberti* (3.7X) (BYU 31956).

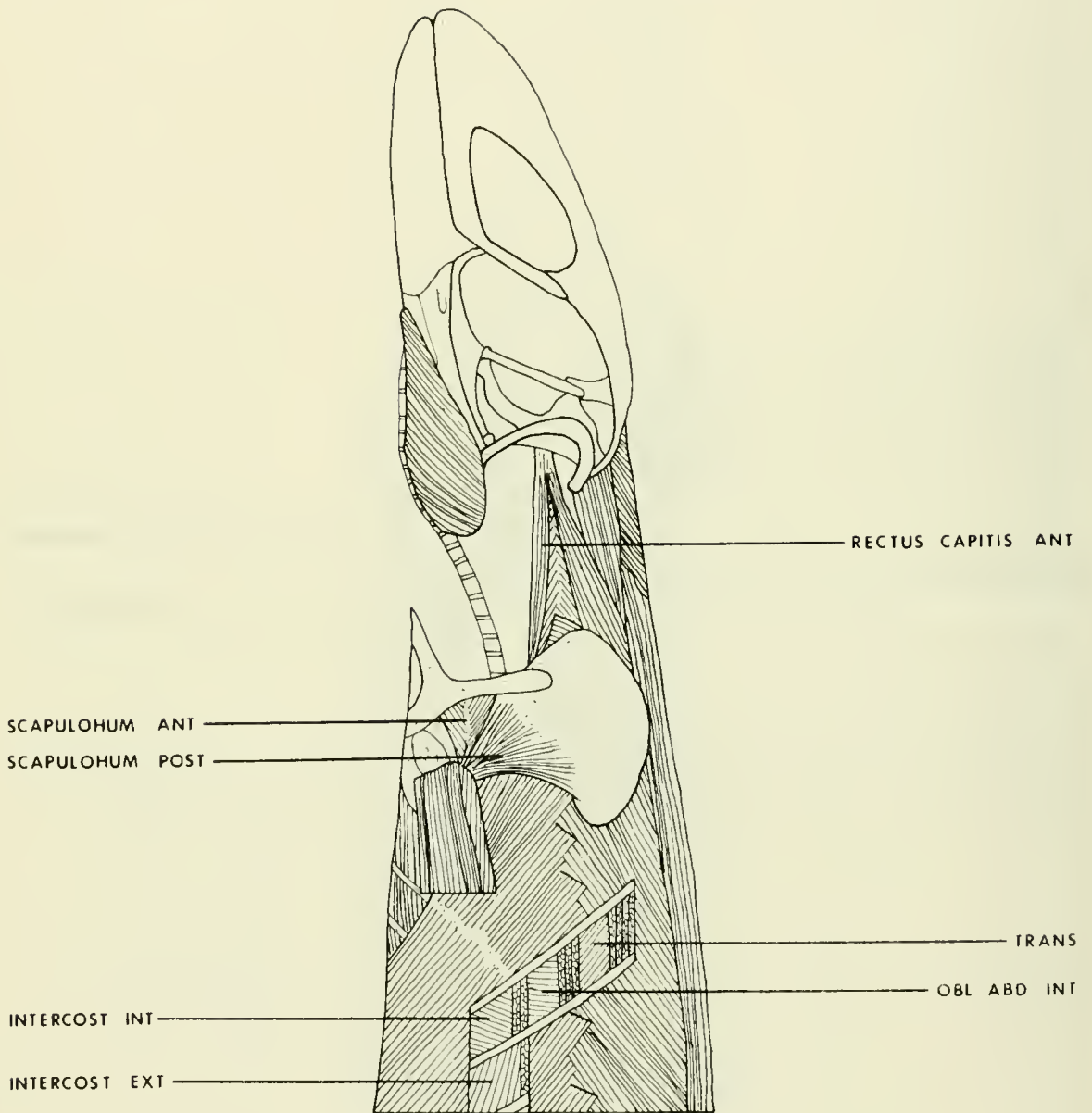
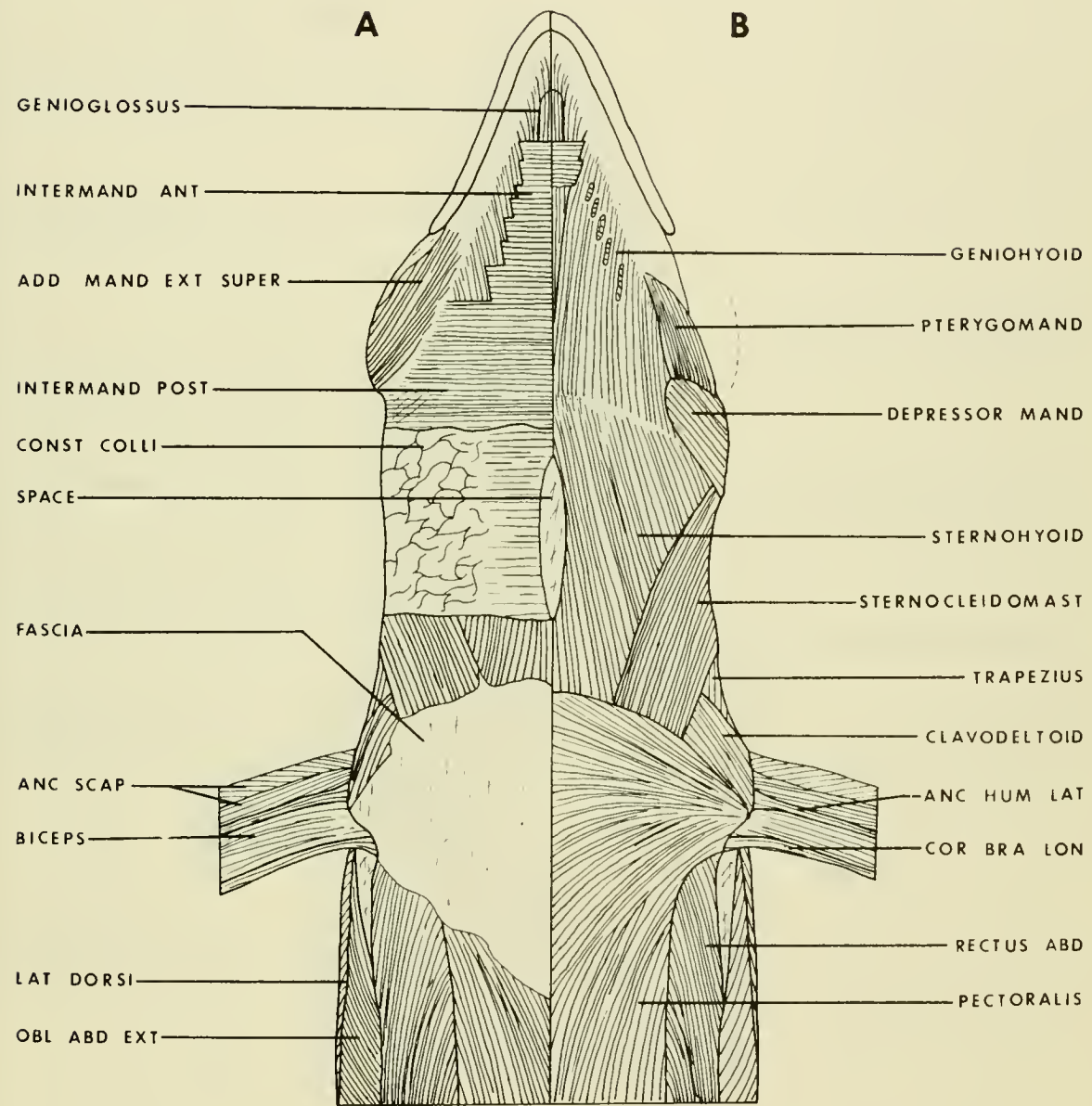
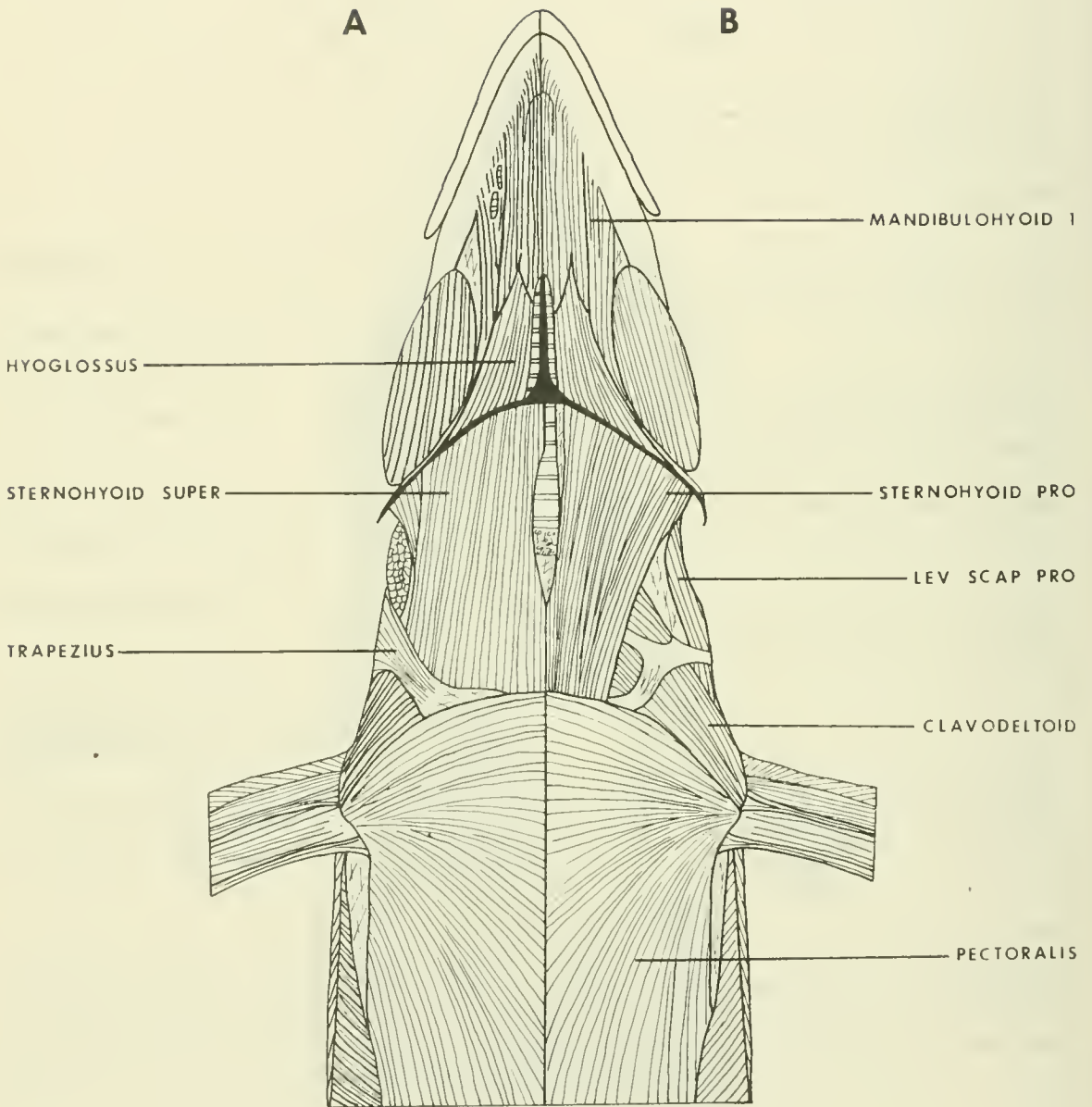


Figure 14. Musculature lateral view, Fifth depth. *Eumeces gilberti* (3.7X) (BYU 31956).



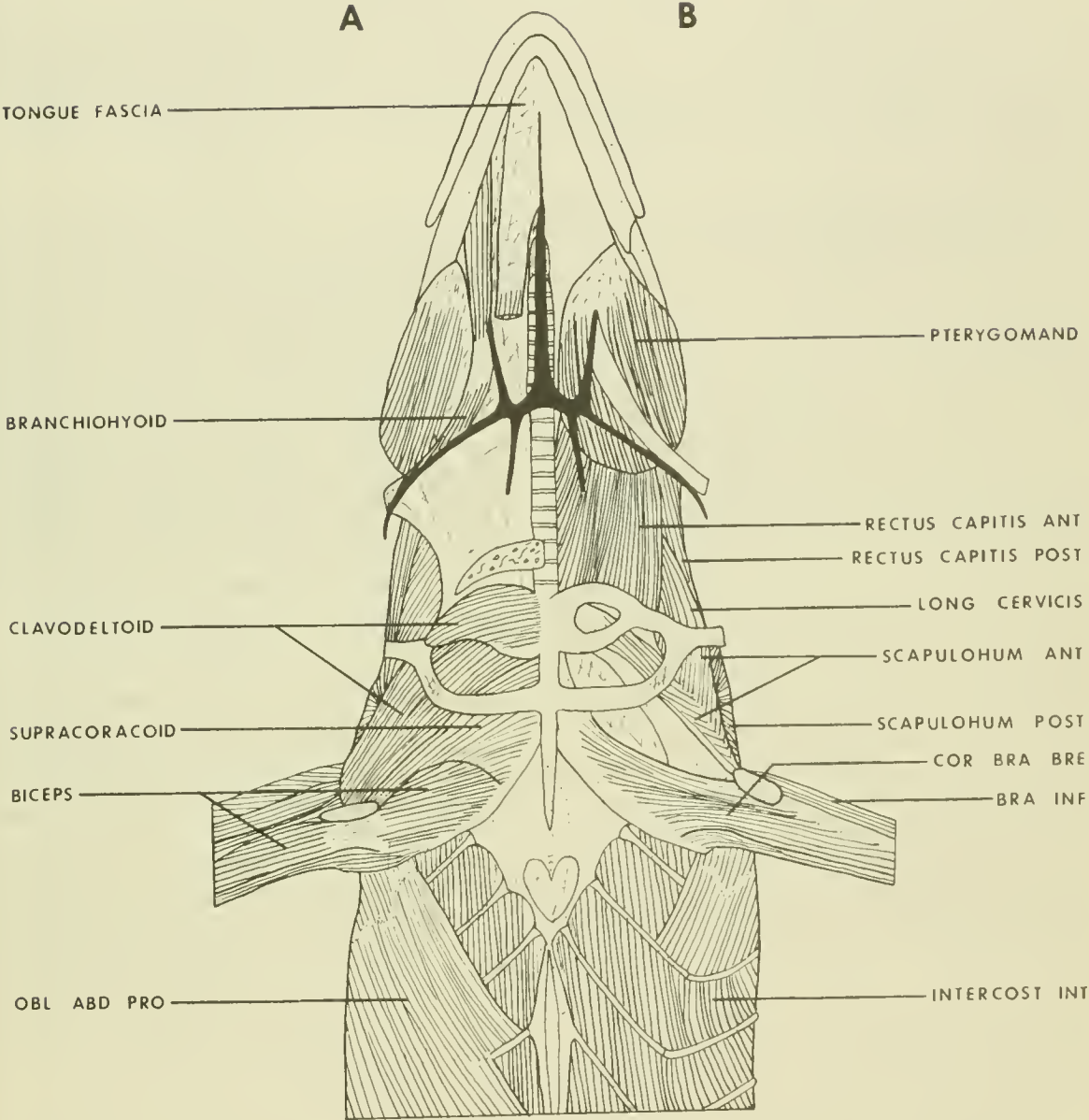
A. Superficial depth
B. First depth

Figure 15. Musculature ventral view. *Eumeces gilberti* (3.7X) (BYU 31956).



A. Second depth
B. Third depth

Figure 16. Musculature ventral view. *Eumeces gilberti* (3.7X) (BYU 31956).



A. Fourth depth
B. Fifth depth

Figure 17. Musculature ventral view. *Eumeces gilberti* (3.7X) (BYU 31956).

DISCUSSION

Osteology

Upon comparing the lizard skull with other groups of the class Reptilia one tends to agree with Jollie (1960) "that all are specialized to some extent and none is strikingly more primitive in the totality of its structure than the others." He further states that the variation of structures can be explained largely by adaptive modification and that the Reptilia show "radiation rather than an anatomical hierarchy of groups."

To determine what the ancestral lizard or the first lizard may have looked like one must rely on the fossil record and the anatomy of living lizards. Broom (1935) is of the opinion that lizards arose from Eosuchian stock in the Upper Triassic and then later developed osteoderms over the skull and the body regions. In the Middle Mesozoic some primitive groups retained the osteoderms while others lost them; thus giving rise to the living forms which have a variety of skull variations. All of the families within the infraorder Leptoglossa (Sincomorpha) have osteoderms except the family Teiidae. The genus *Ameiva* within this family has os palpabre elements (Fisher and Tanner, 1970) which may be suggestive of cranial osteoderms sometime in the past. In families that still retain the osteoderms, Laurtidae and Scincidae, the supratemporal fenestrae are extremely reduced or lost in contrast with the teiids which have large fenestrae. The postfrontals are expanded in the former while in the latter the postfrontals are reduced, lost, or fused with the postorbitals.

Following is a discussion of the osteological comparisons between *E. gilberti* and *E. skiltonianus*. The variations noted are:

1. In *gilberti* the anterior lateral processes of the frontals prevent articulation of the prefrontals with the nasals; whereas, in *skiltonianus* articulation with the nasals and prefrontals can either be present or absent.

2. In *gilberti* the maxillae contain 6 to 8 supralabial foramina and 15 to 20 teeth, average 19; whereas, in *skiltonianus* the maxillae contain 4 to 7 supralabial foramina and 17 to 20 teeth, average 18.

3. In *gilberti* there are 3 to 5 nasal foramina compared with 2 to 4 in *skiltonianus*.

4. In *gilberti* the dentary has 3 to 6 mental foramina and 19 to 23 teeth, average 21; compared with *skiltonianus* which has 4 to 7 mental foramina and 18 to 22 teeth, average 21.

5. In *gilberti* the postorbitals frequently show a reduction of the relative size when compared to other adjacent bones while in *skiltonianus* the same degree of reduction is only occasionally observed. Condensing these variations it is found that: 1. the number of foramina in the maxillae, nasals, and dentary overlap

and are variable within species with neither species showing a definite trend; 2. the same applies to the number of teeth in the maxillae and mandible; 3. in *gilberti* the nasal-prefrontal articulation is constant; whereas, in *skiltonianus* it is variable; and 4. in *gilberti* the postorbitals frequently show a reduction of the relative size when compared to other adjacent bones, whereas, in *skiltonianus* this same degree of reduction is only occasionally observed.

Myology

In contrast with osteology, the homologies of muscles, and thus phylogenies, are difficult to trace when comparing different taxonomic categories. If significant changes are to be found, they are in the cranial and throat myology. These areas seem to be the most easily traceable among groups and in turn are phylogenetically the most important. Brock (1938) working with the genus *Gecko* found the throat musculature to be stable enough for generic discrimination. This conclusion has been supported by other papers by Tanner (1952) with *Plethodontidae*; Robison and Tanner (1962) with *Crotophytus*; Avery and Tanner (1964) with *Sauromalus*; Jenkins and Tanner (1968) with *Phrynosoma*; and Fisher and Tanner (1970) with *Cnemidophorus* and *Ameiva*.

Smith (1960) lists a number of trends which have taken place in the musculature of the more primitive to the more advanced vertebrates. These are: 1. the loss of myosepta and the fusion of myotomes; 2. the separation of muscles into layers; 3. the expansion of muscles from a limited size; 4. the shifting of location of muscles; 5. the multiplication or fusion of muscle attachments; and 6. the subdivision of muscles.

In general these two species show both primitive and advanced characters. The presence of myosepta in the axial musculature would certainly indicate a primitive condition. The subdivision of the intermandibularis anterior, the rectus capitis posterior, the possible trend toward a complete separation of the trapezius and the depressor mandibularis and the distinct layers of the obliquus abdominus externus and sternohyoideus muscles would indicate an advanced condition.

When comparing the myology of these two species little difference is observed. The intermandibularis shows a subspecific difference in *E. skiltonianus*. In two specimens observed of the *E. skiltonianus* subspecies, a range of five to seven subdivisions of the intermandibularis anterior was found. In *E. skiltonianus* the number of subdivisions tends to be toward the lower limit; whereas, in *E. utahensis* the number of subdivisions is toward the higher limit. In contrast both subspecies of *E. gilberti* tend to orient themselves equally with six to seven subdivisions for this

muscle. The only myological character found in this study which differentiates these two species consistently is the depressor mandibularis. In *E. skiltonianus* this muscle is easily separated into an anterior and a

posterior bundle; whereas, in *E. gilberti* this same muscle is somewhat interdigitated and not easily separable. All other muscles mentioned are similar in both species.

SUMMARY AND CONCLUSIONS

The differences observed from the osteology and myology are few and subtle.

Neither species is consistent in having all of the anatomical characters equal. *E. skiltonianus*, however, is more variable than *gilberti*. This species: 1. exhibits a wider range of variation in the number of slips of the intermandibularis anterior; 2. has two distinct bundles of the depressor mandibularis; and 3. has variation in the anterior suture pattern of the frontal, nasal, prefrontal and maxilla elements. *E. gilberti* on the other hand has: 1. only one distinct bundle of the depressor mandibularis; 2. a frequent reduction of the relative size of the postorbitals when compared to other adjacent bones; and 3. a more limited suture pattern in the anterior portion of the skull. The major anatomical difference between these two species seems to be size. From the specimens used in this study the average snout-vent length of *gilberti* is approximately 30mm greater than that of *skilton-*

ianus.

We believe that *skiltonianus* shows more anatomical plasticity than *gilberti*. Plasticity in this case would indicate a more recent gene flow between peripheral and central individuals, and genetic inconsistency which would provide more variation and more flexibility for adaptation and selection. When the geographical distribution of these two species is considered it also appears that *skiltonianus* has more flexibility.

Taylor (1935) has suggested that these species may have arisen simultaneously from a common ancestral stock. On the basis of this anatomical study there is little reason to doubt their close relationship. However, it seems logical to propose an alternate suggestion; namely, that the anatomical variations of *E. skiltonianus*, when compared with similar characters in *E. gilberti*, indicate that *E. gilberti* may have arisen from *E. skiltonianus*.

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OSTEOLOGICAL AND MYOLOGICAL CHARACTERS

by

David F. Avery and Wilmer W. Tanner



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Ctenosaura pectinata (Wiegmann) taken 50 miles S.W. of Guadalajara (Hwy. 80) by Kenneth R. Larsen, 18 July 1970.

EVOLUTION OF THE IGUANINE LIZARDS (SAURIA, IGUANIDAE) AS DETERMINED BY OSTEOLOGICAL AND MYOLOGICAL CHARACTERS

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INTRODUCTION

The family Iguanidae is almost completely restricted to the Western Hemisphere with its main radiations occurring in North and South America. There are also representatives on Fiji, Tonga, and the Galapagos Islands in the Pacific Ocean. Two distinctly related iguanid genera are also found on Madagascar. These genera, *Chalarodon* and *Oplurus*, possess abdominal ribs and are therefore considered to be the most primitive members of the family. Although the iguanid lizards are familiar to most scientists interested in the tropics, their anatomy and evolution are still poorly understood.

Because the family Iguanidae is a large and diverse group of lizards, several distinct phylogenetic lines have been recognized. In this study we are concerned with that group of genera belonging to the iguanine line, which includes the following genera: *Amblyrhynchus* and *Conolophus* from the Galapagos Islands, *Brachylophus* from Fiji and Tonga Islands, *Enyaliosaurus* from Central America, *Ctenosaura* and *Iguana* from Central and South America, *Cychura* from the West Indies, and *Dipsosaurus* and *Sauromalus* from North America.

Those iguanid lizards which have a discontinuous distribution all belong to the iguanine line, or are the most primitive members of the family. Explaining the discontinuous distribution pattern between the Western Hemisphere mainland iguanines, the Pacific Island forms, and their Madagascar relatives has proven to be an enigma for zoogeographers and herpetologists.

The purpose of this study is to establish the degree of relationship between the iguanines of the Galapagos, Fiji, and Tonga Islands with the mainland genera. We will also attempt to define more completely the relationships between the Madagascar genera and the iguanine line. In order to ascertain these relationships, the anterior osteology and myology of each genus has been investigated along with such specialized features as the tongue, hyoid bones, sterna and hemipenes. Hopefully the morphological relationships between the ten genera can be clarified by the use of these relationships, and the evolution and distribution of the iguanine iguanids can be explained. Of all the genera listed above, only *Enyaliosaurus* has not been studied in detail as only two skulls and one complete specimen were available for examination.

LITERATURE

Literature concerning the anatomy of lizards is varied, widely scattered and incomplete. Because of the large amount of material dealing with this subject, this discussion will be limited, with some exceptions, to that literature which pertains to those anatomical features treated in this paper; namely the anterior osteology and myology, hyoid bones, sternum, the tongue, and the hemipenes.

One of the earliest discussions of the head-osteology or myology of lizards is that of Mivart (1867) who published a detailed account of the myology of *Iguana tuberculata* (Iguanidae). This work was followed by Mivart's (1870) paper on the myology of *Chamaeleon parsonii* (Chamaeleonidae). The latter is detailed and when used with his paper on *Iguana* con-

stitutes two of the most complete discussions of lizard myology in the literature.

Sanders (1870) published an account of the myology of *Platydactylus japonicus* (Gekkonidae) which is a comprehensive presentation but lacks adequate illustrations. Sanders (1872) again published a lizard myology, with an account on the musculature of *Liolepis belli* (Agamidae). As with the earlier papers of Mivart, the paper is well illustrated. Gervais (1873) published a brief note on the skull and teeth of the Australian agamid *Molock*. Notes and illustrations dealing with the myology of *Phrynosoma coronatum* (Iguanidae) were related by Sanders (1874).

Parker (1880) described the skull of *Lacerta agilis*, *L. viridis* and *Zootoca vivipara* (Lacertidae). That

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work was followed by De Vis's (1883) paper on the myology of *Chlamydosaurus kingii* (Agamidae). Unfortunately, his paper was poorly illustrated.

Boulenger (1885 to 1887) published his monumental catalogue of lizards in the British Museum in which are scattered his observations on the osteology of lizards, including a discussion of the distinctive cranial features of *Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura* and *Iguana* (Iguanidae). Gill (1886) reviewed Boulenger's classification system for lizards and summarized the important osteological differences between the families. Boulenger (1890) further summarized his osteological observations on the distinctive cranial characters of the iguanid lizards related to *Iguana*. Even at this early stage of investigation, the iguanine line of evolution was recognized in the family Iguanidae as a natural group. All seven genera listed by Boulenger are today still considered to be iguanines. Boulenger (1891) published a series of remarks concerning the osteology of *Heloderma* and presented a conclusion for the systematic position of the family Helodermatidae.

E. D. Cope was also actively publishing on lizard anatomy during this period. Cope (1892a) commented on the homologies of the posterior cranial arches in reptiles, and his conclusions in this matter have laid the foundation for understanding the components of the posterior skull of lizards by later workers. During the same year, Cope's (1892b) classic work on lizard osteology was published. Not only does Cope provide a comparison of the cranial osseous elements, but he describes in detail osteological features of the iguanines, *Dipsosaurus* and *Sauromalus*. This material was also incorporated into Cope's (1900) comprehensive taxonomic work.

The German worker Siebenrock, during the close of the 19th century, made several contributions to our knowledge of the anatomy of lizards. He published a brief paper on the skeleton of *Uroplatus fimbriatus* (Gekkonidae) (1892a) and a more lengthy discussion on the skulls of skinks, anguids and *Gerrhosaurus* (Cordylidae) (1892b). These papers were followed by Siebenrock's (1893) discussion of the skeleton of *Brookesia superciliaris* (Chamaeleonidae); an account of the skeleton of *Lacerta simonyi* (Lacertidae) (1894); and a comprehensive discussion on the skeleton of the agamid lizards (1895).

Bradley (1903) discussed the muscles of mastication and the movement of the skull in lizards. Broom (1903) named *Paliguana whitei* (Eosuchia) from the Triassic beds of South Africa. This find is of considerable importance as it may represent an animal ancestral to lizards. The presence of this fossil also establishes the great geologic age of lizards in general. He also studied (1903b) the development of pterygoquadrate arch in lizards. Following these investigations, Beddard (1905) published notes on the skull of *Uromastix* (Agamidae), and in a separate paper dis-

cussed some aspects of *Chlamydosaurus kingi* and other agamids. Kingsley (1905) examined the reptile jaw bones and figured the medial surface of the *Iguana* (Iguanidae) mandible. Beddard (1907) examined the internal anatomy of several genera of lizards and described the uniqueness of various characters to particular families.

Bryant (1911) revised the iguanid genus *Phrynosoma* and its synonym *Anota*. In this paper he presented some osteological observations on the species and genera treated in the study.

A most useful paper on the phylogeny of jaw muscles in vertebrates was published by Adams (1919). Although the paper is concerned with reptiles in general it describes the jaw musculature of *Iguana* (Iguanidae) and *Varanus* (Varanidae) in particular. Kesteven (1917) analyzed the pterygoids and parasphenoids of reptiles and amphibians.

Rice (1920) described the development of the skull in the skink *Eumeces quingialineatus*. Camp (1923) published his classic work on the classification of lizards, based on their anatomy. In this account, Camp figured the throat musculature of *Sphenodon* (Rhynchocephalia), *Amphisbaenia* (Amphisbaenidae), *Coleonyx* (Eublepharidae), *Uroplatus* (Gekkonidae), *Typhlops*, (Typhlopidae), *Tupinambis* (Teiidae), *Varanus* (Varanidae), *Gerrhosaurus*, *Zonorus*, *Chamaesaura* (Cordylidae), *Lialis* (Pygopodidae), *Brachyllophus*, *Phrynosoma* (Iguanidae), *Calotes* (Agamidae), *Chamaeleon* (Chamaeleonidae), *Xantusia* (Xantusiidae), *Trachysaurus* (Scincidae), *Lacerta* (Lacertidae), *Heloderma* (Helodermatidae), *Gerrhonotus* (Anguinidae), *Xenosaurus* (Xenosauridae), *Anniella* (Anniellidae), and *Gekko* (Gekkonidae). Reese (1923) analyzed the osteology of *Tupinambis nigropunctatus* (Teiidae).

Broom (1924) discussed the origin of lizards by tracing the cranial elements of the fossil forms *Youngina*, *Mesosuchus*, and *Paliguana* (eosuchia). These genera were compared with modern skinks, chamaeleonids, varanids and agamids. Broom indicated the closeness of *Paliguana* to the modern lizards and suggested ways whereby *Paliguana* could have evolved into recent forms.

Dubeeq (1925) discussed the elevating muscles of the lower jaws in reptiles, and Williston published his treatise on the osteology of reptiles. This latter work is of interest as Williston figured skulls of *Conolophus* (Iguanidae), *Varanus* (Varanidae), *Amphisbaena* (Amphisbaenidae), and a chamaeleon. He also classified the Squamata in the Subclass Parapsida with the lizardlike fossil *Araeoscelis*.

Gilmore (1928) summarized the fossil lizards of North America and discussed the osteology of many forms as well as establishing the existence of some families of lizards in North America as early as the Upper Cretaceous. Nopcea (1928) presented a synopsis of the genera of reptiles. For each family he cited

osteological characteristics and summarized the fossil and recent genera found in each. Lastly, Sinitsin (1928) analyzed skulls in the family Teiidae and separated the family into two divisions based on cranial osteology.

Goodrich (1930) published his major work on the structure and development of the vertebrates. In it he figured and described the skulls of *Varanus* (Varanidae) and *Lacerta* (Lacertidae). Edgeworth (1931a, 1931b) presented two papers on reptile anatomy in which he discussed the development of the eye, masticatory and hyoid muscles of *Sphenodon* (Rhynchocephalia) and an account of muscles used in opening and shutting the mouth of vertebrates. His remarks in the second paper were restricted to the lizard genera *Lacerta* (Lacertidae), *Platydictylus* (Gekkonidae), and *Calotes* (Agamidae). Brock (1932) continued early investigations on lizard anatomy and the developmental stages in the skulls of the geckos *Lygodactylus capensis* and *Pachydactylus maculosa*. Kingman (1932) studied the skull of the skink, *Eumeces obsoletus*.

Davis (1934) published a laboratory manual for *Crotaphytus* (Iguanidae) which was one of the most complete studies on lizard anatomy. In the year 1935 important papers on lizard anatomy were published by Brock, Broom, and Edgeworth. Brock's discussion dealt with the problem of temporal bones in lizards, birds, and mammals. Most of Brock's comments were relegated to skinks and geckos. Broom's work also dealt with the temporal bones and correlated the information known for the fossil *Paliguana* and *Youngina* (Eosuchia) with the structure of the modern genera *Iguana* (Iguanidae), *Agama* (Agamidae), *Cnemidophorus*, *Teiis*, *Callopiestes* (Teiidae), *Varanus* (Varanidae), *Scapteira* (Lacertidae), *Gerrhosaurus*, *Zonurus*, *Platysaurus* (Cordylidae), *Gerrhonotus*, *Anguis* (Anguinidae) and *Uroplatus* (Gekkonidae). The highlights of the year, for lizard anatomists, was the publication of Edgeworth's (1935) classic work on the cranial muscles of vertebrates. In this paper he describes the myology of *Iguana* (Iguanidae) and correlates it with members of the related families of lizards Chamaeleonidae and Lacertidae.

Davis (1936) reviewed problems of muscle terminology in reptiles. Howell (1936) presented a comprehensive study on the shoulder of reptiles. Much of the description contained in the paper pertains to the shoulder of *Iguana* (Iguanidae). Bahl (1937) published a comprehensive paper on the skull of *Varanus* (Varanidae). This is one of the most detailed accounts of lizard osteology in the literature.

Brock (1938) presented a discussion of the cranial muscles of geckos and El Toubi analyzed the osteology of *Scincus scincus* (Scincidae). The final paper of the decade was Evans' (1939) discussion of the evolution of the atlas-axis complex. This paper not only discussed fossil reptiles but also provided an account

of the atlas-axis complex as it exists in *Sphenodon* (Rhynchocephalia) and *Iguana* (Iguanidae). In a later paper (1941a) he analyzed the skull of the chamaeleon *Lophosaura ventralis*, and in a second paper (1941b) the skull of *Acontias* (Scincidae) and the affinities between snakes and lizards. During the same year Gilmore (1941) published accounts of fossil lizards of the iguanid genus *Aciprion* from the Oligocene formations of Wyoming. In this paper he indicated the affinities of *Aciprion* to the more recent genus *Crotaphytus* (Iguanidae). Malam (1941) provided a description of the cranial anatomy of *Gerrhosaurus* (Cordylidae).

Angel's (1942) synopsis of Madagascar lizards was published and the skeletal characteristics of *Chalarodon* and *Ophurus* (Iguanidae) were reviewed. Hoffstetter (1942) reviewed the remains of fossil iguanids from the Eocene and Oligocene of Europe. Iyer, during the same year described the skeleton of *Calotes versicolor* (Agamidae). Mittleman (1942) presented a taxonomic summary of the genus *Urosaurus* (Iguanidae). He also discussed the general evolution of North American members of the family Iguanidae, and on the basis of osteology broke the family into lines of evolution, presenting a phylogenetic tree, in which he placed *Ctenosaura* as a primitive ancestral type from which two main lines of evolution were formed. One line contained the sceloporine lizards and *Phrynosoma* while the other contained the crotaphytine lizards including *Dipsosaurus* and *Sauromalus*. Mittleman also indicated that *Dipsosaurus*, *Sauromalus* and *Ctenosaura* are all very closely related.

The genus *Uromastix* (Agamidae) has been a popular subject of investigation among Old World workers. In 1942 the bony palate of this agamid was described and figured by Saksena. During the same year Young published on the cranial morphology of *Xantusia* (Xantusiidae). DuBois (1943) analysed the skull of *Cnemidophorus* (Teiidae) and Iyer (1943) followed his earlier work with a detailed description of the skull of *Calotes versicolor* (Agamidae).

Kestevens' major paper on the evolution of the skull and cephalic muscles appeared in 1944. The musculature was described for *Physignathus*, *Amphibohurus* (Agamidae), *Anolis*, *Basiliscus* (Iguanidae), *Chamaeleon* (Chamaeleonidae), *Tiliqua* (Scincidae), *Varanus* (Varanidae), and *Sphenodon* (Rhynchocephalia). In the same year Zangerl examined the skull of the Amphisbaenidae. In this paper are figured skulls of *Amphisbaena*, *Bipes*, *Geocalamus*, *Monapeltis*, *Leposternon*, and *Trogonophis*. *Prolacerta* (Eosuchia) and the Protorosaurian reptiles were discussed by Camp (1945) who indicated that the Lower Triassic *Prolacerta* is intermediate between *Youngina* (Eosuchia) and modern lizards. In the same year Zangerl completed his analysis of the Amphisbaenidae with a discussion of the postcranial skeleton.

Pletzen (1946) examined the cranial morphology

of *Cordylus* (Cordylidae) and discussed the cranial kinesis of that lizard. The genus *Xenosaurus* (Xenosauridae) was the topic of study for Barrows and Smith (1947). The authors described the osteology in detail and concluded that this lizard has affinities with the family Anguidae but should be retained in its own family. El Toubi (1947) published two papers; one describes the osteology of *Agama stellio* (Agamidae), and the other discusses the cranial osteology of *Uromastix aegyptia* (Agamidae).

Broom (1948) described and figured the skull of *Phrynosoma cornutum* (Iguanidae). George (1948) examined the musculature of *Uromastix hardwickii* (Agamidae). The latter paper is accompanied by excellent figures dealing with limb musculature. El Toubi (1949) completed his investigation of *Uromastix aegyptia* (Agamidae) and published an account of the post cranial osteology. Mahendria (1949) described in detail the skull of the gecko *Hemidactylus flaviviridis*.

Several papers were published in 1950 dealing with lizard anatomy. Bellairs presented the cranial anatomy of *Anniella* (Anniellidae); Detrie analyzed the skull of *Phrynosoma cornutum* (Iguanidae); Haines discussed the flexor muscles in the forearm and hand of lizards and mammals; Stokely surveyed the occurrence of the intermedium wrist bone in lizards; and Toerien also presented an account of the cranial morphology of *Anniella* (Anniellidae).

Only two papers dealing with lizard anatomy were published in 1951. Norris and Lowe discussed the osteology and myology of *Phrynosoma m'callii* (Iguanidae) and figured parts of the skull of several *Phrynosoma*. Webb presented the cranial anatomy of the geckos *Palmatogecko rangei* and *Oedura karroica*.

El toubi and Khalil (1952) summarized the structure of the cranium in Egyptian geckos. Barry (1953) added some observations to the cranial anatomy of *Agama* (Agamidae); and Brattstrom (1953) outlined the occurrence of Pleistocene lizards from California. Among the forms listed in Brattstrom's paper are skeletal remains of *Sceloporus*, *Crotaphytus* (Iguanidae), *Cnemidophorus* (Teiidae), and *Eumeces* (Scincidae).

George (1954) dealt with the cranial osteology of the agamid *Uromastix hardwickii* and figured the skull. McDowell and Bogert (1954) studied the skeletons of *Lanthanotus* (Lanthanotidae), and compared it with *Shinisaurus*, *Xenosaurus*, *Melanosaurus* (Xenosauridae), *Heloderma* (Helodermatidae), *Varanus* (Varanidae), *Aigialosaurus* (Aigialosauridae), *Tylosaurus* (Mososauridae), *Python* (Boidae), *Leptotyphlops* (Leptotyphlopidae), *Typhlops* (Typhlopidae), *Pygopus*, *Delma*, *Lialis*, *Aprasia*, *Ophioseps* (Pygopodidae), *Aristelliger* (Gekkonidae), *Coleonyx* (Eublepharidae), *Xantusia* (Xantusidae), *Cordylus*, *Gerrhosaurus* (Cordylidae), *Peltosaurus*, *Diploglossus*, *Gerrhonotus*, *Anguis*, *Abronia*, *Celestus* (Anguinidae), and *Anniella*

(Anniellidae). The authors were able to present a phylogeny for the Anguinomorphian lizards. This paper is well illustrated and is probably one of the best anatomical studies performed on lizards since Camp's paper in 1923. Poglayen-Newall discussed the jaw musculature of lizards in the same year.

Edinger (1955) discussed the parietal foramen in reptiles as to function and size and figured the skull roof of *Iguana* (Iguanidae). George (1955) completed an earlier work on *Uromastix hardwickii* (agamidae). In his paper the postcranial osteology is discussed. Hoffstetter (1953) in the reptile volume of the French treatise on Paleontology reviewed general osteological features of the lizard skull and presented a summary of fossil lizard remains from Europe. Also Hotton (1955) surveyed the dentition and diets of North American Iguanidae. His analysis of teeth confirms the suspected close relationship between *Dipsosaurus*, *Sauromalus* and *Ctenosaurus*. Islam's description (1955) of the skull of *Uromastix hardwickii* (Agamidae) is one of the most comprehensive yet presented for that genus.

The iguanid genus *Amblyrhynchus* was revised by Eibl-Eibesfeldt (1956). In this review the dorsal aspect of the skull of *A. c. cristatus* is figured. Islam completed his analysis of the skeleton of *Uromastix hardwickii* (Agamidae) in the same year. He described and figured aspects of the postcranial skeleton. Oelrich (1956) published his excellent, well illustrated account of the anatomy of the head of *Ctenosaura pectinata* (Iguanidae). In the same year Romer published his monumental work on the osteology of the reptiles. Besides giving a general account of the evolution of the reptile skeleton, Romer figured the skulls of *Varanus* (Varanidae), *Iguana* (Iguanidae), *Brookesia* (Chamaeleonidae), *Chalcides* (Scincidae), *Xantusia* (Xantusidae), *Cordylus* (Cordylidae), *Amphisabaena* (Amphisbaenidae), and *Typhlops* (Typhlopidae).

Lundelius (1957) analyzed skeletal adaptations in *Sceloporus* (Iguanidae) and figured the skull. Brattstrom (1958) published two papers on fossil lizards. He recorded *Crotaphytus*, *Sceloporus*, *Sauromalus* (Iguanidae), and *Cnemidophorus* (Teiidae) from the Pleistocene sediments of California and in a second paper *Aciprion* (Iguanidae) from the Oligocene formations of Wyoming. Savage (1958) investigated the genera *Urosaurus* and *Uta* (Iguanidae). After an anatomical analysis of iguanids Savage was able to separate the family into a sceloporine line and an iguanine line of evolution. The iguanine line is characterized by having an "S"-shaped nasal passage. Besides the eight iguanine genera outlined earlier, Savage included *Crotaphytus* in the iguanine line of evolution.

El Toubi and Kamal (1959) presented a well detailed and illustrated discussion of the skull of *Chalcides ocellatus* (Scincidae). The following year Haas (1960) presented a discussion of the trigeminus

muscles of *Xenosaurus* and *Shinosaurus* (Xenosauridae). This paper is detailed and filled with exact illustrations. Hofer (1960) compared the skulls of *Tupinambis* (Teiidae) and *Varanus* (Varanidae). Jollie's discussion (1960) of the head skeleton of lizards is an excellent summary of evolution in that saurian. Besides detail, this paper contains illustrations of the skulls of *Tupinambis* (Teiidae), *Amphisbaena* (Amphisbaenidae), *Anguis* (Anguinidae), and *Uromastix* (Agamidae). Lastly, Smith (1960) treated the theoretical development of chordate evolution of the lizard skeletons and musculature in detail.

Colbert (1961) published his book on the evolution of the vertebrates. In it he discussed the problem of lizard affinities with other reptiles and places them with the Diapsida. The paper by Sukhanov (1961) investigated the musculature of lizards and concluded it to be of two types: Scinco-Geckomorphous and Iguanomorphous. The author then presented a phylogeny of lizard families depending on their type of musculature.

Skeletal variations in *Sator grandaevus* (Iguanidae) were summarized by Etheridge (1962) while Kluge (1962) discussed the comparative osteology of *Coleonyx* (Eublepharidae). This latter paper is highly detailed and well illustrated. Another discussion of lizard anatomy was that of Robison and Tanner (1962) who outlined the anterior osteology and myology of *Crotaphytus* (Iguanidae). This paper is also well illustrated.

Estes (1963) reported on fossil lizards from the Miocene strata of Florida. Among those genera found were *Leiocephalus* (Iguanidae), *Eumeces* (Scincidae), *Cnemidophorus* (Teiidae) and unidentified Iguanidae, Gekkonidae and Anguinidae. Also during 1963, Harris' paper on the anatomy of *Agama agama* (Agamidae) was published. This is a well illustrated account in the form of a laboratory guide. Osteology and myology of the anterior body regions are well covered. Ostrum (1963) presented a short discussion on the lack of herbivorous lizards in the modern fauna. He indicated that this is probably because of the difficulties in eating caused by the streptostylic and kinetic nature of the skull.

Avery and Tanner (1964) described the anterior osteology and myology of *Sauromalus obesus* (Iguanidae). This paper has several illustrations of that region. Brattstrom (1964) identified fossil lizards from cave deposits in New Mexico. Estes (1964) in a major publication described the fossil vertebrates from the Late Cretaceous Lance Formation of Wyoming. We note that no Iguanidae were recorded and that some of Gilmore's (1928) Cretaceous iguanids were transferred to other families. Estes and Tihen (1964) recorded Miocene-Pliocene vertebrates from Nebraska and listed among their finds *Phrynosoma* (Iguanidae), *Cnemidophorus* (Teiidae), *Eumeces* (Scincidae), and *Gerrhonotus* (Anguinidae). Ether-

idge (1964) discussed the fossil record of Late Pleistocene lizards from the West Indies, *Thecadactylus* (Gekkonidae), *Leiocephalus*, *Anolis* (Iguanidae), *Ameiva* (Teiidae), and a braincase from an iguanine type lizard are listed among the remains. Etheridge (1964) also examined the skeletal morphology of the sceloporine lizards and presented a phylogenetic tree for the sceloporines. He removed *Crotaphytus* from the iguanine line of Savage (1958) and allied it to the sceloporines and *Phrynosoma*. He also indicated from osteological data, that the iguanine line of evolution is a natural grouping. Eyal-Giladi (1964) described the development of the chondrocranium of *Agama stellio* (Agamidae). Hollman (1964) described some Pleistocene amphibians and reptiles from Texas. The fauna does not differ appreciably from the modern fauna. Tilak (1964) reported on the osteology of *Uromastix hardwickii* (Agamidae).

Blanc (1965) described the skeleton of the Madagascar iguanid, *Chalarodon*. Etheridge (1965) examined some fossil lizards from the Dominican Republic and listed among the remains *Aristelliger* (Gekkonidae), *Anolis*, *Leiocephalus* (Iguanidae), *Ameiva* (Teiidae), and *Diploglossus* (Anguinidae). Duellman (1965) utilizing external morphology suggests a close relationship between *Enyaliasaurus* and *Ctenosaura* (Iguanidae). Gelback (1965) presented a most useful paper summarizing the Pliocene and Pleistocene amphibians and reptiles from North America. The paper also has an excellent bibliography. Ray (1965) analyzed the number of marginal teeth in *Ctenosaura* and *Anolis*. Weiner and Smith (1965) examined the osteology of the crotaphytiform lizards and illustrated the skulls of that group of iguanids.

Etheridge (1966) dealt with the systematics of *Leiocephalus* as based on the osteology of that iguanid genus. Lateral views of the mandibles are figured. Romer (1966) published his third edition of "Vertebrate Paleontology" which contains a summary of the evolution of lizards as well as illustrations of the skulls of *Youngina*, *Prolacerta* (Eosuchia), *Sphenodon* (Rhynchocephalia), and *Polyglyphanodon* (Iguanidae).

The morphological literature of 1967 includes a paper by Duda comparing the cranial osteology of *Agama tuberculata* (Agamidae) with the skulls of other agamids; and a discussion by Etheridge of the caudal vertebrae of lizards.

Criley (1968) described the cranial osteology of the Gerrhonotiform lizards and Gasc (1968) analyzed the osteology and morphology of *Dibamus novae-guineae* (Dibamidae). Iordansky (1968) discussed the muscles of the external ear in lizards in one paper, and cranial kinesis in the skulls of lizards in a second paper. The osteology and myology of *Phrynosoma platyrhinos* and *P. hernandesi* (Iguanidae) was treated by Jenkins and Tanner (1968) in a well illustrated paper. Montanucci (1968) compared the dentition of

the iguanid lizards *Iguana*, *Ctenosaura*, *Enyaliosaurus* and *Basiliscus* and Secoy (1968) described the myology of *Sceloporus clarki* (Iguanidae). Romer (1968) presented a summary of lizard relationships to other reptiles and analyzed the fossil lizards of the Mesozoic.

Presch (1969) analyzed the evolution of species in the genus *Phrynosoma* (Iguanidae) by utilizing osteology.

Fisher and Tanner (1970) compared the head and thorax morphology of the Teiids (*Cnemidophorus* and *Ameiva*), and Nash and Tanner (1970) compared the head and thorax anatomy of Skiltons and Gilberts skinks, genus *Eumeces* (Scincidae).

In summary the literature dealing with anterior osteology and myology of lizards is scattered and varied. Descriptions of skulls representing almost all families can be found. With the exception of such papers as Camp (1923), McDowell and Bogert (1954), Savage (1958), Etheridge (1964), and Presch (1969), little has been done, utilizing osteology, to analyze the evolutionary lines within families. The myology of lizards is even less well known with no attempt having been made to analyze the musculature of a particular family or evolutionary line within a family.

The fossil record of lizards is very incomplete, as indicated by the above summary, but the fossil record does indicate that lizards have been in existence since Triassic time and in North America since Cretaceous time. Little has been done to trace the degree of change between fossil osteology and recent genera.

Besides dealing with the osteology and myology of the head region, this paper utilizes the anatomy of the sternum. Some of the earliest discussions of the sternum are those of Howes (1891) and Parker (1891), who described the sterna of fossil reptiles. Sabatier (1897) examined reptile sterna and clavicles, and commented on their origin. One of the most complete, early attempts at discussing the osteology of the sternum, was that of Hanson (1919) who described the sterna of *Cnemidophorus* (Teiidae), *Anguis* (Anguinidae), *Stellio* (Agamidae), *Varanus* (Varanidae), *Chirotes* (Amphisbaenidae), *Chamaeleo* (Chamaeleonidae), *Draco*, *Calotes* (Agamidae), and *Iguana* (Iguanidae).

Camp (1923) described the sterna of lizards in detail. He presented a summary of all elements as found in the recognized families and figured the sterna of *Gerrhosaurus* (Cordylidae), *Xenosaurus* (Xenosauridae), *Bachia* (Teiidae), and *Xantusia* (Xantusiidae). Gladstone and Wakeley (1932) presented a survey of the morphology of the sternum and its relationship to the ribs. Reese (1923) figured the sternum of *Tubinambis* (Teiidae). El Toubi (1947) included a description of the sternum in his account of the osteology of *Agama stellio* (Agamidae). The same author published a photograph of the sternum of *Uromastix aegyptia* (Agamidae) in 1949.

Islam (1956) figured the sternum of *Uromastix*, and Romer (1956) in his "Osteology of the Reptiles" discusses the evolution of the sternum and figures that of *Lacerta* (Lacertidae), and *Bachia* (Teiidae). Savage (1958) utilized the sternum in his discussion of *Uta* and *Urosaurus* (Iguanidae). He figured the sterna of both genera.

Potter (1961) described and figured the sternum of *Phrynosoma* (Iguanidae) as did Kluge (1962) for *Coleonyx* (Eublepharidae). Etheridge (1964) examined and figured the sterna of *Phrynosoma*, *Uma*, *Calisaurus*, *Holbrookia*, *Petrosaurus*, *Uta*, *Urosaurus* and *Sator* in his analysis of the evolution of the sceloporine line of iguanids and in 1965 discussed the abdominal skeletons of lizards and figured sterna and ribs of *Stenocercus*, *Amblyrhynchus*, *Anolis* and *Chalarodon* (Iguanidae). In the latter paper Etheridge notes four patterns of attachment of ribs to sterna, which is of value in separating the various groups of iguanid lizards. Weiner and Smith (1965), in their discussion of the crotaphytiform lizards, figured the sterna of two species of *Crotaphytus*. The sternal structure of *Leiocephalus* (Iguanidae) was also discussed by Etheridge (1966). The sternum and ribs of *Phrynosoma* (Iguanidae) are rediscussed by Jenkins and Tanner (1968) and Presch (1969) presented and figured the sterna of *Petrosaurus*, *Uma* and *Phrynosoma* (Iguanidae).

The tongue and associated hyoid elements of lizards have received more attention than has the sternum. The earliest papers on the lizard hyoid or tongue are those of Lasana (1834) and Minot (1880). Each author presented a general discussion of hyoid elements in reptiles. Cope (1892), in his "Osteology of the Reptiles" discussed the hyoid bones and figured those of *Sphenodon* (Rhynchocephalia), *Chamaeleon* (Chamaeleonidae), *Gekko*, *Aristelliger*, *Phyllodactylus*, *Thecadactylus* (Gekkonidae), *Eublepharis* (Eublepharidae), *Calotes*, *Phrynocephalus*, *Uromastix* (Agamidae), *Holbrookia*, *Phrynosoma*, *Sceloporus*, *Uta*, *Sauromalus*, *Crotaphytus*, *Anolis*, *Ctenosaura*, *Iguana* (Iguanidae), *Anguis*, *Dracaena*, *Gerrhonotus*, *Opisaurus* (Anguinidae), *Heloderma* (Helodermatidae), *Xenosaurus* (Xenosauridae), *Varanus* (Varanidae), *Scincus*, *Eumeces*, *Egernia*, *Liolepisma*, *Gongylus* (Scincidae), *Celestes* (Anguinidae), *Gerrhosaurus*, *Zonurus* (Cordylidae), *Mancus* (Lacertidae), *Tubinambis*, *Cnemidophorus* (Teiidae), *Anniella* (Anniellidae), *Chirotes*, *Amphisbaena* and *Rhineura* (Amphisbaenidae). Cornig (1895) discussed the tongue musculature of reptiles and Chaine (1902) analyzed the musculature in the region of the hyoids. Although his paper is very general, he does describe some of the muscles of *Chamaelon* (Chamaeleonidae). Beddard (1905) figured and described the hyoid bones of *Chlamydosaurus kingi* and *Physignothus* (Agamidae). Gandolfi (1908) described the tongue of agamids and iguanids. The musculature of the tongue

of *Agama*, *Amphibolurus*, *Calotes*, *Liolaemus* (Agamidae), *Iguana* and *Cyclura* (Iguanidae) are described. Camp (1923) also dealt with hyoids and tongues in his tome on lizard classification. The tongues were described in general and the hyoids of *Coleonyx* (Eublepharidae), *Uroplatus* (Gekkonidae), *Brachylophus* (Iguanidae), *Calotes* (Agamidae), *Phrynosoma* (Iguanidae), *Gerrhonotus* (Anguinidae), *Gerrhosaurus*, *Chamaesaura*, *Zonurus* (Cordylidae), and *Xenosaurus* (Xenosauridae) were figured. Reese (1923) described and figured the tongue of *Tupinambis* (Teiidae) and Sewertzoff (1929) described the tongues of reptiles in general and proposed a phylogeny based on them. The tongue of *Lacerta* (Lacertidae), *Ascalabotes* (Gekkonidae), *Ophisaurus*, *Anguis* (Anguinidae), *Ablepharus* (Scincidae), *Varanus* (Varanidae), *Ameiva* (Teiidae), *Calotes* (Agamidae), and *Chamaeleo* (Chamaeleonidae) were discussed and figured. Ping (1932) described the tongue of *Hemidactylus bourigii*. The hyoids and tongues of *Hemidactylus* (Gekkonidae), *Mabuya* (Scincidae), *Cabrita* (Lacertidae), *Varanus* (Varanidae), *Anolis* (Iguanidae), *Calotes* (Agamidae), *Sitana*, *Draco* (Agamidae), and *Chamaeleon* (Chamaeleonidae) were discussed and illustrated by Gnanamuthu (1937), as was the hyoid of *Agama stellio* (Agamidae) by El Toubi (1947). The tongue of the anguimorphs *Gerrhonotus* (Anguinidae), *Shinisaurus* (Xenosauridae), *Varanus* (Varanidae), *Heloderma* (Helodermatidae) and *Lanthanotus* (Lanthanotidae) were analyzed by McDowell and Bogert (1954). Oelrich (1956) described the hyoid of *Ctenosaura* (Iguanidae). Romer (1956) has also treated the hyoids of lizards and illustrated those of *Heloderma* (Helodermatidae) and *Basiliscus* (Iguanidae). The hyoids of Indian reptiles were described by Sondhi (1958) who figured the hyoid and tongue of *Varanus* (Varanidae). Jollie (1960) described the hyoid of many genera of lizards and figured that of *Amphisbaena* (Amphisbaenidae). Goin and Goin (1962) figured the tongues of *Mabuya* (Scincidae), *Varanus* (Varanidae), *Tachydromus* (Lacertidae), *Ophisaurus* (Anguinidae), *Calotes* (Agamidae), *Gekko* (Gekkonidae), *Nessia* (Scincidae) and *Dibamus* (Dibamidae). Kluge (1962) described the hyoid of *Coleonyx* (Eublepharidae) and Tilak (1964) presented the hyoid of *Uromastix* (Agamidae). Presch (1969) illustrated the hyoids of *Phrynosoma coronatum* and *Sceloporus magister* (Iguanidae).

The hemipenes have been considered by a few workers as being of evolutionary importance. One of the earliest comprehensive discussions is that of Cope (1896), who described the hemipenes of several genera of lizards and was able to create a key to separate some genera of Iguanidae by their hemipenes. Camp (1923) also utilized the hemipenes in his classification system. He also summarized Cope's work. Ortenburger (1923) suggested a method for preparing reptilian hemipenes for study. McCann

(1946) also treated the subject of hemipenes in reptiles. The hemipenes of *Uromastix hardwickii* was examined by Charles (1953) and Majupuria (1957). Dowling and Savage (1960) discussed in detail the hemipenis of snakes. Their paper is a classic and is a primary source of information on structure and vocabulary concerning reptile hemipenes. The latest work on hemipenes is that of Rosenberg (1967) who described those structures in the Amphisbaenidae.

Several other approaches have been used in studying the problem of saurian phylogeny. One structure that has been examined is the ear of lizards. Smith (1938) studied evolutionary changes in the middle ear of some agamids and iguanids. Baird (1960) surveyed the periotic labyrinth of reptiles. Hamilton (1964) examined the gross structure of the inner ear of lizards and was able to divide lizards into four groups on the basis of their ear structures. Schmidt (1964) examined the phylogenetic significance of the lizard cochlea and from his study was able to make some phylogenetic groupings between families.

Histological evidence is also useful in interpreting iguanid phylogeny. Hebard and Charipper (1955) studied the adrenal glands of several genera of lizards. The authors' work shows the natural grouping of lizards at family level and confirms the phylogenetic conclusions of Camp (1923) based on osteology and myology. The thyroid glands of iguanids and agamids were compared by Lynn, O'Brien and Herhenreder (1966). They concluded that both families are closely related.

In a study of pinworms in lizards, Gambino (1957) and Gambino and Heyneman (1960) found that the most primitive pinworms are specific to *Dipsosaurus*, *Sauromalus*, *Ctenosaura*, and *Enyaliosaurus*.

A further approach to saurian phylogeny has been through karyotype study. Several papers have described the karyotype of different genera of lizards but the paper by Gorman, Atkins and Holzinger (1967) is most useful in phylogenetic interpretations. Fifteen genera were examined, including *Ctenosaura*, *Cyclura*, *Iguana* and *Sauromalus* of the iguanine line. They found that the karyotype evolution in iguanids has been quite conservative and there appears to be very little difference in the chromosomes of the genera from Madagascar, Brazil, the Antilles and North America.

The results of such methods of study as histology, parasitology and cytology are suggestive but not sufficiently specific to be definitive. The complete solution to the problems of iguanid phylogeny must come therefore from studies of gross anatomy and particularly from osteology and myology.

The problems of iguanine distribution have been discussed by Beaufort (1951), Darlington (1957) and Carlquist (1965). All three considered the Pacific iguanids as waif populations resulting from rafting but were at a loss to explain the presence of iguanids

on Madagascar.

The plausibility of Continental Drift and its effect on ancient flora and faunas have recently been detailed by Hurley, Almeida, Melcher, Cordani, Rand, Kawashita, Vandomos, Pinson and Fairbairn (1967), Heirtzler (1968), Maxwell (1968), Hurley and Rand (1969), Kurten (1969), and McElhinny and Luck

(1970). These authors have reviewed the history of the drift theory and presented new evidence consisting of comparative radiometric ages, sea-floor spreading, and paleomagnetism. The fossil remains from Antarctica, Africa, and South America have also been cited.

MATERIAL AND METHODS

The descriptions of the osteology of the ten genera investigated are based on four or more skulls and jaws and two or more sterna and hyoids from each group. In all cases skeletons were cleaned by soaking in 50% ammonium hydroxide after defleshing, and then boiled for one to three hours in water and cleaned by hand. Final cleaning of sutures and bleaching was accomplished by immersion in Chlorox bleach for a few minutes. Many of the museum specimens were obtained as skeletons and required no cleaning.

One or two specimens of each genus were used for myological studies. All are preserved in 10% formalin or 70% alcohol. Tongues, hyoids, and hemipenes were

removed from specimens destined to be skeletonized or from individuals on whom the myological studies had been completed. All three structures were preserved and stored in 70% alcohol.

All specimens are accessioned in one or another of the natural history collections of the following institutions: American Museum of Natural History (AMNH), Brigham Young University (BYU), University of Kansas (KU), Museum of Comparative Zoology, Harvard University (MCZ), Southern Connecticut State College (SCSC), and U. S. National Museum (USNM). Below is a summary list of materials utilized for this study.

Osteology

- Amblyrhynchus cristatus* Bell
AMNH 24978, Galapagos Islands
AMNH 75943, Galapagos Islands
AMNH 76197, Galapagos Islands
BYU 22810, Galapagos Islands
MCZ 2006, Charles Island, Galapagos Islands
- Brachylophus fasciatus* Cuvier
BYU 23743, Nukualofa, Tonga Island
MCZ 5222, Fiji Islands
MCZ 15008, Vunisea, Kadavu Island, Fiji Islands
MCZ 15009, Vunisea, Kadavu Island, Fiji Islands
- Chalarodon madagascariensis* Peters
MCZ 11508, Tulear, S. W. Madagascar
MCZ 11522, Tulear, S. W. Madagascar
MCZ 11531, Tulear, S. W. Madagascar
MCZ 11532, Tulear, S. W. Madagascar
- Conolophus subcristatus* (Gray)
AMNH 50797, Galapagos Islands
AMNH 50798, Galapagos Islands
AMNH 71304, Galapagos Islands
MCZ 2027, Albrmarle Island, Galapagos Islands
- Conolophus pallidus* Heller
MCZ 79772, Galapagos Islands
- Ctenosaura hemilopa* (Cope)
BYU 30272, St. Esteban Island, Gulf of California
- Ctenosaura pectinata* (Wiegman)
BYU 22796, San Blas, Nayarit, Mexico
MCZ 11350, Colima, Mexico
MCZ 2176, Acapulco, Mexico
MCZ 24904, Tepic, Mexico
- Cyclura carinata* Harlan
MCZ 59255, Sand Cay, Turks Island
- Cyclura cornuta* (Bonnaterre)
AMNH 57878, No data, probably Haiti
AMNH 57968, No data, probably Haiti
- Cyclura macleayi* Gray
MCZ 6915, Santiago, Cuba
- Enyaliosaurus clarki* (Bailey)
USNM 48965, No data
- Enyaliosaurus palearis* (Stejneger)
USNM 21452, No data

- Dipsosaurus dorsalis* Baird and Girard
AMNH 79962, Palm Springs, California
BYU 21726, Palm Springs, California
BYU 23760, Palm Springs, California
BYU 23761, Palm Springs, California
- Iguana iguana* Wiegman
BYU 22795, El Zacatal, Campeche, Mexico
BYU 22852, San Blas, Nayarit, Mexico
MCZ 54989, Gorge of Tortugero, Costa Rica
SCSC 506, Finca Toboga, Guanacaste Province, Costa Rica
- Iguana delicatissima* Laurenti
MCZ 83228, St. Eustatius
- Oplurus sebae* (Dumeril and Bibron)
MCZ 3336, No data
MCZ 37188, Majunga, Madagascar
MCZ 37191, Majunga, Madagascar
MCZ 37192, Majunga, Madagascar
- Sauromalus obesus* (Baird)
BYU 21734, Glen Canyon, Utah
BYU 23762, St. George, Utah
MCZ Z3335, 35 miles West Sonoita, Sonora, Mexico
MCZ 8894, Buckskin Mountains, Arizona
- Sauromalus hispidus* Stejneger
MCZ 79777, Angel de La Guarda Island, Gulf of California
- Sauromalus shawi* Cliff
MCZ 85533, Isla San Marcos, Gulf of California
- Sauromalus varius* Dickerson
MCZ Z3331, No data
BYU 30269, St. Esteban Island, Gulf of California
BYU 30270, St. Esteban Island, Gulf of California
BYU 30271, St. Esteban Island, Gulf of California

Myology

- Amblyrhynchus cristatus* Bell
BYU 22806, Galapagos Islands
BYU 22810, Galapagos Islands
- Brachylophus fasciatus* Cuvier
BYU 23743, Nukualofa, Tonga Island
BYU 31955, Nukualofa, Tonga Island

Chalarodon madagascariensis Peters

BYU 2280t, Tulea, Madagascar

BYU 22803, Tulea, Madagascar

Conolophus suberistatus (Gray)

BYU 2281t, Galapagos Islands

Ctenosaura pectinata (Wiegman)

BYU 22796, San Blas, Nayarit, Mexico

BYU 22850, San Blas, Nayarit, Mexico

Cyclura nuchalis Barbour and Noble

BYU 22799, North Cay, Bahama Islands

Dipsosaurus dorsalis Baird and Girard

BYU 21726, Palm Springs, California

BYU 22855, Palm Springs, California

BYU 23760, Palm Springs, California

BYU 23761, Palm Springs, California

BYU 31954, Mesquite, Nevada

Enyaliosaurus clarki (Bailey)

KU 62447, Mexico

Iguana iguana Wiegman

BYU 22795, El Zacatal, Campeche, Mexico

BYU 22851, San Blas, Nayarit, Mexico

BYU 22853, San Blas, Nayarit, Mexico

Oplurus sebae (Dumeril and Bibron)

BYU 11504, Andrambovato, Madagascar

Sauromalus obesus (Baird)

BYU 21734, Glen Canyon, Utah

BYU 23762, St. George, Utah

BYU 31953, St. George, Utah

OSTEOLOGY

An examination of the osseous elements of the iguanine lizards and the Madagascar iguanids reveals the following structures.

Skull and Jaws

The superficial elements of the skull of the iguanines and the Madagascar iguanids have been examined in detail. The analysis of the skull bones and jaws was made from two approaches. One approach was to examine the size of the bones by measuring length and width of each bone and then computing a percentage between length and width, which was then compared with similar data for identical bones in other genera. Tables representing the means and the ranges of these values for each genus are presented throughout this chapter. All measurements are in millimeters.

A second approach to the study of the skull was made through observations and comparisons of the shape of the bones and their relationship to other bones. A summary of these observations and comparisons is presented in the text of this chapter. All observations and measurements are based on four to six individuals from each genus.

The skull of the iguanine lizard is streptostylic with a freely movable quadrate bone which articu-

lates dorsally with the paroccipital process and ventrally with the quadrate process of the pterygoid. Such movement can be demonstrated in fresh and preserved specimens of all the genera examined. In general it may be said that the iguanine skull forms a compact and light, yet very strong cage for the brain and sense organs of the head.

The general shape of the skull is either elongated and flattened dorsoventrally or shortened and flattened laterally. Measurements of the length of the skull were taken from the tip of the premaxillary bone to the most posterior extension of the occipital condyle. Width of the skull was taken at the widest extension between the suborbital bars in the area of the orbit. Height measurements were taken at the posterior end of the maxillary bone and extending to the skull roof directly above that point. A summary of the ranges and means of these measurements is presented in Tables 1 and 2.

A survey of the means presented in those tables indicates that *Amblyrhynchus* (length-width, .789, length-height, .460) has the shortest and widest skull, whereas the longest and lowest skull is found among the continental genera *Sauromalus*, *Ctenosaura*, and *Cyclura*. Table 2 indicates that *Sauromalus* (.286) has the flattest skull of the iguanines, followed closely by *Ctenosaura* (.316) and *Cyclura* (.326) which also have a low skull roof.

TABLE 1
SKULL LENGTH AND WIDTH

Genus	Length			Width			Width-Length Ratio		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
<i>Amblyrhynchus</i>	41	4-47	7-53.2	30.3	36	7-43.1	.732-	.789-	.809
<i>Brachylophus</i>	27.7	30.7	34.2	16.8	19.8	24.9	.535-	.644-	.726
<i>Chalarodon</i>	12.5	13.1	14.1	8.8	9	2-10.0	.666-	.705-	.792
<i>Conolophus</i>	85	0-79	1-86.0	37.0	54	1-64.3	.618-	.679-	.747
<i>Ctenosaura</i>	30.1	40.5	54.1	17	6-24.0	32.1	.584-	.593-	.605
<i>Cyclura</i>	45.7	73	3-97.1	26.7	43.6	56.6	.582-	.593-	.623
<i>Dipsosaurus</i>	22.2	22.3	23.9	14.0	16	6-18.3	.700-	.745-	.781
<i>Iguana</i>	49	3-60.0	70.3	28.1	35.4	36.5	.519-	.549-	.590
<i>Ophirus</i>	18	1-21.6	30.6	11.2	14.5	20.0	.608-	.670-	.729
<i>Sauromalus</i>	23.4	34	4-48.1	14.3	22.6	32.8	.611-	.653-	.684

TABLE 2
SKULL LENGTH AND HEIGHT

Genus	Length			Width			Width-Length Ratio		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
<i>Amblyrhynchus</i>	41	4-47	7-53.2	20.8	23	2-26.0	.402-	.460-	.489
<i>Brachylophus</i>	27.7	30.7	34.2	11.2	12.0	13.8	.372-	.390-	.404
<i>Chalarodon</i>	12.5	13.1	4.1	4.4	4-8	5.1	.335-	.368-	.400
<i>Conolophus</i>	85	0-79	1-86.0	20.6	30.5	34.3	.344-	.379-	.398
<i>Ctenosaura</i>	30.1	40	5-54.1	9	7-12.8	16.4	.303-	.316-	.331
<i>Cyclura</i>	45	7-73	3-97.1	15.2	23	9-24.6	.306-	.326-	.334
<i>Dipsosaurus</i>	22.2	22	3-23.9	7.3	8.6	9.4	.365-	.386-	.400
<i>Iguana</i>	49	3-60.0	70.3	17	6-20.6	22.6	.318-	.344-	.356
<i>Ophirus</i>	18	1-21	6-30.6	6.4	7	7-10.3	.336-	.357-	.386
<i>Sauromalus</i>	23.4	34	4-48.1	6.8	9	9-14.1	.273-	.286-	.308

For the sake of convenience the skull has been divided into a posterior occipital segment and an anterior maxillary segment.

The occipital segment forms a median axis for the attachment of the neck and articulation of the remainder of the skull. It consists of two parts, (a) the braincase (basisphenoid, basioccipital, prootic, exoccipital, supraoccipital, and the associated semicircular canals), and (b) the foramen magnum (enclosed by the basioccipital, exoccipital and supraoccipital). A tripartate occipital condyle is located on the posterior end of the basioccipital and the lateral exoccipital in all genera of iguanine lizards.

Basisphenoid

Basisphenoid (Figures 1 and 2) forms a portion of the floor of the braincase, is bordered posteriorly by the basioccipital, and is attached dorsally to the prootic bone. Anteriorly the bone is expanded into two anterolateral basipterygoid processes which articulate laterally, with the pterygoid bones. Anteromedially the basisphenoid is extended forward as the parasphenoid process. The basisphenoid forms points of origin for the inferior part of the protractor pterygoideus muscle.

Measurements of the length of the basisphenoid were made from the suture between basisphenoid and basioccipital, to the beginning of the parasphenoid process. Width was computed as the distance between the widest extension of the basipterygoid processes. An examination of the ratio means in Table 3 reveals that the lowest ratio is possessed by *Chalarodon* (.360) while the highest is that of *Ophurus* (.755). Among the New World genera, *Dipsosaurus* (.469) has the lowest ratio and *Iguana* (.652) has the highest. A low ratio indicates that the bone is much longer than wide, whereas the higher ratios indicate bones that have lengths and widths almost equal.

Observations of the bone's position in the skull indicates some variability in the articulation between basipterygoid process and the pterygoid bone. This articulation occurs medial and posterior to an expansion of the pterygoid bone just posterior to the ptery-

goid's midpoint. This point of articulation is almost completely obscured ventrally by the pterygoid bone in *Amblyrhynchus*, *Chalarodon*, and *Ophurus*. In *Dipsosaurus* the articulation is visible ventrally but occurs dorsal to the ventral border of the pterygoid. In *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cychura*, *Iguana* and *Sauromalus* the anterior articulating portion of the basipterygoid process is partially obscured and two thirds of the articulation occurs on the ventromedial border of the pterygoid bones, rather than on the medial face.

Basioccipital

Basioccipital (Figures 1 & 2) forms part of the occipital condyle and the posterior floor of the braincase. It is the main point of attachment for ventral axial musculature. Anteriorly the basioccipital joins the basisphenoid and dorsolaterally it attaches to the exoccipitals and the prootic bones. The third bundle of the longissimus dorsi muscle attaches here.

Length and width measurements were made of the basioccipital with the length being taken from the suture between the basisphenoid and basioccipital to the posterior tip of the occipital condyle. The width of the bone was considered as the distance between the tips of the lateral extensions of the sphenoccipital tubercles. An examination of the ratio means in Table 4 indicates that the highest ratios for the basioccipital are possessed by *Brachylophus* (.709), *Ctenosaura* (.664), *Amblyrhynchus* (.663), and *Sauromalus* (.649) while *Dipsosaurus* (.369) and *Conolophus* (.477) possess the lowest ratios. High ratios denote that lengths and widths are nearly equal for the bone.

TABLE 3
BASISPHENOID BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	5.1- 6.0- 7.0	9.1-12.8-16.7	.419-.482-.560
<i>Brachylophus</i>	4.1- 4.5- 5.0	6.9- 7.9- 9.5	.526-.570-.594
<i>Chalarodon</i>	1.0- 1.1- 1.3	2.8- 2.9- 3.2	.333-.360-.406
<i>Conolophus</i>	7.5-10.5-12.1	13.2-19.9-23.9	.506-.533-.567
<i>Ctenosaura</i>	3.9- 5.3- 7.4	6.7- 8.3-10.7	.549-.633-.691
<i>Cychura</i>	6.2-10.0-14.4	10.3-16.1-22.3	.546-.619-.685
<i>Dipsosaurus</i>	2.5- 2.9- 3.7	5.4- 6.3- 6.9	.412-.469-.536
<i>Iguana</i>	7.2- 7.9- 8.7	10.3-12.2-14.5	.600-.652-.699
<i>Ophurus</i>	2.5- 3.4- 5.1	3.4- 4.5- 6.6	.717-.755-.780
<i>Sauromalus</i>	3.8- 5.7- 8.1	6.7- 9.6-12.2	.500-.589-.669

TABLE 4
BASIOCCIPITAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	8.7- 9.8-11.6	12.3-15.0-17.6	.573-.663-.739
<i>Brachylophus</i>	5.0- 6.2- 7.4	3.5- 4.2- 5.0	.648-.709-.781
<i>Chalarodon</i>	2.0- 2.1- 2.2	3.2- 3.4- 3.6	.600-.625-.656
<i>Conolophus</i>	8.5- 9.4-10.7	15.0-20.0-23.4	.420-.477-.580
<i>Ctenosaura</i>	4.2- 5.7- 6.7	6.2- 8.6-10.5	.650-.644-.677
<i>Cychura</i>	6.2- 9.4-12.1	11.6-15.1-24.2	.500-.534-.596
<i>Dipsosaurus</i>	2.1- 2.2- 2.5	5.9- 6.1- 6.7	.350-.369-.389
<i>Iguana</i>	6.6- 8.1- 9.8	11.5-16.0-19.6	.500-.513-.573
<i>Ophurus</i>	3.1- 3.3- 4.0	5.4- 5.7- 6.4	.534-.583-.625
<i>Sauromalus</i>	3.4- 5.8- 7.8	5.1- 9.8-13.0	.600-.649-.696

Prootic

Prootic bones form the anterolateral wall of the braincase and contain the elements of the ear. Posteriorly, the prootic is bordered by the supraoccipital, basisphenoid, basioccipital, and the exoccipital. The anterior portion of the bone is surrounded by membranes that contain the optic nerve. The pseudotemporalis and protractor pterygoideus muscles originate

on the prootic bone. Because of difficulties in measuring, the prootic was not studied in detail.

Exoccipital

Exoccipitals bones form the posterolateral wall of the braincase and the lateral parts of the occipital condyle. Mediolateral articulations form with the parietal, supratemporal and quadrate bones. The exoccipital also articulates at its most lateral projection with the prootic bone. The longissimus dorsi and episternocleidomastoideus muscles insert on the paraoccipital process of the bone.

The length of the exoccipital bone was measured from the lateral wall of the foramen magnum to the point of articulation by the paraoccipital process with the squamosal and quadrate bones. Width is represented as the distance between the exoccipital articulation with the supraoccipital bone and the union with the basioccipital at the occipital condyle. As Table 5 indicates, the lowest ratio means for exoccipitals are possessed by *Dipsosaurus* (.594) and *Conolophus* (.626). The largest ratios are found in *Brachylophus* (.858), *Amblyrhynchus* (.830), and *Chalarodon* (.813). As with the other bones, near equal relationships between length and width are expressed as high ratios.

TABLE 5
EXOCCIPITAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	8.9-11.0-13.0	8.5-11.6-16.0	.762-.830-.861
<i>Brachylophus</i>	5.0- 5.5- 6.3	4.5- 4.7- 5.0	.793-.858-.900
<i>Chalarodon</i>	2.2- 2.2- 2.4	1.8- 1.8- 1.9	.782-.813-.863
<i>Conolophus</i>	8.5-12.4-14.2	13.0-20.0-23.8	.571-.626-.653
<i>Ctenosaura</i>	3.0- 4.9- 6.9	4.5- 7.8-12.5	.552-.649-.724
<i>Cyclura</i>	6.2-11.3-15.8	8.5-17.1-25.8	.605-.661-.720
<i>Dipsosaurus</i>	2.8- 3.3- 3.6	5.4- 5.6- 5.8	.509-.594-.648
<i>Iguana</i>	7.0- 7.7- 8.2	9.4-11.2-11.9	.606-.671-.744
<i>Oplurus</i>	3.3- 3.9- 5.0	4.2- 5.1- 6.8	.735-.774-.809
<i>Sauromalus</i>	4.0- 5.6- 8.2	5.3- 8.2-12.4	.602-.692-.759

Supraoccipital

Supraoccipital (Figures 3 & 4) forms the roof of the posterior part of the braincase and the dorsal rim of the foramen magnum. It articulates with the prootic bone anterolaterally, the exoccipital posteriorly, and the parietal at its anterior extreme.

The supraoccipital lengths were measured as the distance between its posterolateral sutures with the exoccipital bones in the area of the foramen magnum. The width was measured as the distance between the suture with the parietal bone anteriorly, and the dorsal lip of the foramen magnum posteriorly. Table 6 indicates that the genera possessing supraoccipitals with the lowest ratios include *Chalarodon* (.583), *Oplurus* (.675), and *Sauromalus* (.680), while the highest ratios are found in *Brachylophus* (.982) and *Iguana* (.979).

TABLE 6
SUPRAOCCIPITAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	6.4- 6.8- 7.8	9.0- 9.8-11.9	.655-.700-.755
<i>Brachylophus</i>	5.5- 5.9- 6.1	5.2- 5.4- 5.6	.852-.906-.982
<i>Chalarodon</i>	1.2- 1.5- 2.1	2.4- 3.0- 3.7	.413-.524-.583
<i>Conolophus</i>	11.4-14.7-21.1	7.4-13.5-13.9	.648-.706-.793
<i>Ctenosaura</i>	3.3- 4.7- 6.7	5.1- 6.9- 9.2	.632-.677-.739
<i>Cyclura</i>	5.8-10.9-14.6	8.1-14.4-18.1	.700-.751-.806
<i>Dipsosaurus</i>	3.7- 4.0- 4.2	4.6- 4.8- 5.2	.795-.820-.874
<i>Iguana</i>	7.9- 8.6- 9.6	7.6- 8.8- 9.4	.900-.949-.979
<i>Oplurus</i>	2.4- 3.2- 5.0	4.0- 5.2- 7.4	.521-.596-.675
<i>Sauromalus</i>	3.3- 4.6- 6.8	5.1- 7.2-10.0	.538-.632-.680

Orbitosphenoid

Orbitosphenoid is a vertical element surrounding the optic foramen. The anterior border forms the posterior margin of the optic foramen and the inferior process forms an area of origin for the superior rectus muscles at the eye. The orbitosphenoid also has connections with the prootic bone and the alar process of the basisphenoid. It was found to be absent in most of the cleaned skulls in the collections examined.

The combination of bones in the anterior region of the skull is referred to as the maxillary segment. It consists of four parts, (a) the palate (pterygoid, ectopterygoid, vomer, palatine, premaxilla, and maxilla), (b) orbits (frontal, postfrontal, and jugal), (c) nasal capsule (nasal, prefrontal, lacrimal, and septomaxilla), and (d) temporal fenestra (parietal, supratemporal, postorbital, squamosal, quadrate and epipterygoid). These bones are discussed as listed above.

Pterygoid

Pterygoid (Figures 1, 2, 3, 4, 5 and 6) extends posteriorly as the posterior part of the palate. The pterygoids are paired bones sutured at the anterior end of the palatines, anterolaterally to the ectopterygoids and posteromedially to the basisphenoids. They comprise a major area of motion between the occipital and maxillary regions as the posterolateral portions articulate with the quadrate which is movable. Articulating with the pterygoid on the dorsal border of the quadrate projection is the columella. At the ventral border, the pterygoid forms the posterior limit of the oral cavity and contributes an area for the origin of the pterygomandibularis muscle. On the dorsal ridge, medial to the columellar fossa, is an area of insertion for the levator pterygoideus muscle. The insertion of most of the protractor pterygoideus muscle is located on the medial surface of the quadrate process of the pterygoid bone. The posterior fibers of the pterygomandibularis muscles arise along the ventrolateral border of the lateral side of the quadrate process.

Measurements taken of the pterygoid bone include length; represented as the distance between the anterior portion of the pterygoid where it sutures with the

palatine and the most posterior tip of the quadrate process; and the width as the distance between the articulation with the basiptyergoid process of the basisphenoid bone and the suture with the ectopterygoid bone. Table 7 summarizes these measurements and a survey of the ratio means indicates that the lowest pterygoid ratio (long, narrow bones) are possessed by *Cyclura* (.283), *Sauromalus* (.293), and *Iguana* (.309). The highest ratios (short, wide bones) are found in *Brachylophus* (.458) and *Chalarodon* (.435). The unique relationships of the pterygoid to the basiptyergoid process of the basisphenoid bone have already been reviewed. The shape of the medial border of the pterygoid also controls the shape of the pyriform recess (Figs. 1 and 2) of the palate. This shape varies from a gradually widening slit as seen in *Brachylophus*, *Chalarodon* and *Ophurus* to a more severe and rapid change in width of the recess as seen in *Amblyrhynchus*, *Conolophus*, and *Cyclura*. The remaining genera are intermediate between the above conditions.

TABLE 7
PTERYGOID BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	23.9-28.8-32.6	8.4-10.3-13.5	.309-.346-.414
<i>Brachylophus</i>	14.0-15.5-18.4	6.1- 7.0- 7.5	.380-.458-.535
<i>Chalarodon</i>	5.6- 5.7- 5.7	2.4- 2.4- 2.6	.421-.435-.464
<i>Conolophus</i>	34.2-51.0-59.5	11.8-18.8-22.3	.345-.367-.382
<i>Ctenosaura</i>	18.7-24.5-33.5	5.8- 7.5-10.8	.287-.311-.355
<i>Cyclura</i>	29.1-39.0-63.1	7.3-13.5-20.6	.250-.283-.326
<i>Dipsosaurus</i>	10.1-12.0-13.1	4.1- 4.2- 5.3	.333-.353-.404
<i>Iguana</i>	26.5-31.5-35.6	7.0- 9.5-11.1	.264-.309-.364
<i>Ophurus</i>	8.4-11.6-19.6	2.9- 3.9- 6.2	.316-.347-.377
<i>Sauromalus</i>	13.0-19.8-30.0	3.9- 5.8- 9.1	.252-.293-.343

Ectopterygoid

Ectopterygoid (Figs. 1, 2, 3, 4, 5 and 6) forms a brace between the palate and the external roofing bones. Laterally the ectopterygoid sutures with the jugal and the posterior process of the maxilla, and mesially with the pterygoid. Dorsally it forms the posterolateral part of the floor of the orbit.

TABLE 8
ECTOPTERYGOID BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	7.2- 8.9-10.4	1.8- 2.4- 3.1	.250-.275-.303
<i>Brachylophus</i>	3.0- 4.0- 5.0	1.0- 1.5- 2.2	.333-.371-.440
<i>Chalarodon</i>	1.4- 1.4- 1.5	0.6- 0.6- 0.7	.400-.431-.466
<i>Conolophus</i>	10.9-15.3-17.5	5.0- 6.5- 7.5	.405-.429-.458
<i>Ctenosaura</i>	3.3- 5.6- 8.9	1.4- 2.3- 3.6	.404-.421-.444
<i>Cyclura</i>	6.1-10.8-15.2	2.2- 4.1- 6.3	.356-.377-.414
<i>Dipsosaurus</i>	2.3- 2.6- 2.8	1.4- 1.5- 1.8	.551-.600-.642
<i>Iguana</i>	6.1- 7.9- 9.3	3.0- 3.5- 4.0	.415-.448-.491
<i>Ophurus</i>	2.2- 2.6- 3.6	0.9- 1.1- 1.5	.409-.419-.434
<i>Sauromalus</i>	2.4- 5.4- 8.5	1.0- 2.0- 3.2	.323-.392-.457

Measurements made on the ectopterygoid include the length, taken as the distance between the suture with the pterygoid and the suture with the jugal and maxilla. The width was measured as the greatest diameter of the bone at its point of union with the jugal and maxilla. These measurements are summarized in Table 8 and an examination of the ratio means shows that the lowest ratio (long, narrow bones) is found in *Amblyrhynchus* (.275) and the form with the highest ratio (short, wide bones) is *Dipsosaurus* (.600).

Vomers

Vomers (Figs. 1 and 2) are paired bones forming the most anterior part of the palate, the medial borders of the fenestra vomeronasalis externus and the medial borders of the fenestra exchoanalis. Posteriorly the vomer is attached to the palatines and dorsally to the medial surface of the maxilla. Medially the vomers support the nasal septum and the cartilage of Jacobson's organ. At the extreme anterior end the vomer sutures with the premaxilla.

The length of the vomer was measured from the anterior suture with the premaxilla to the most posterior point of the suture with the palatine bone. Width of the vomer was the distance between the medial border of the vomer at the ventral midline and the most lateral border where it attached to the maxilla. Table 9 summarizes the measurements of vomer bones and the ratio means show that the shortest, widest, vomers (highest ratios) are possessed by *Chalarodon* (.711) and the narrowest longest vomers (lowest ratios) are possessed by *Amblyrhynchus* (.253), *Cyclura* (.274), and *Ctenosaura* (.278).

The vomers possess a small blunt projection that protrudes from the lateral border of the bone into the opening of the fenestra exchoanalis and fenestra vomeronasalis externa and separates the opening. The possession of this anterolateral projection is seen in all ten genera. Some genera have a secondary projection which extends into the lumen of the fenestra vomeronasalis externa. This projection can be seen in *Brachylophus*, *Ctenosaura*, *Cyclura*, *Iguana*, and in *Sauromalus*.

TABLE 9
VOMER BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	11.2-13.0-15.0	2.8- 3.2- 4.0	.200-.253-.294
<i>Brachylophus</i>	6.5- 7.0- 7.6	2.4- 2.5- 2.7	.315-.359-.380
<i>Chalarodon</i>	1.8- 1.9- 2.0	1.3- 1.3- 1.4	.700-.711-.722
<i>Conolophus</i>	12.2-13.6-17.1	4.1- 5.5- 7.0	.335-.372-.409
<i>Ctenosaura</i>	7.2- 9.7-11.1	2.0- 2.9- 4.2	.270-.278-.328
<i>Cyclura</i>	11.6-18.2-25.8	3.1- 5.5- 7.7	.235-.274-.335
<i>Dipsosaurus</i>	3.9- 4.2- 4.8	2.0- 2.1- 2.3	.479-.497-.512
<i>Iguana</i>	13.5-17.4-21.1	4.8- 5.5- 6.9	.265-.322-.389
<i>Ophurus</i>	3.1- 4.2- 6.0	1.4- 1.6- 2.2	.365-.399-.451
<i>Sauromalus</i>	5.7- 7.8-11.8	1.4- 2.6- 3.7	.245-.329-.390

Palatine

Palatine (Figs. 1, 2, 3, and 4) bones form the main part of the palate, the floor of the orbit and nasal capsule. This bone has three processes; the anterior or vomerine, forms the posterior floor of the olfactory capsule; the pterygoid process, which attaches dorsally to the pterygoid, forms the medial rim of the inferior orbital fossa and the floor of the orbit; and the maxillary process attaches dorsally to the prefrontal and ventrally to the jugal and maxillary bones.

The length of the palatine was taken as the distance from the anterior suture with the vomer bone at the midline to the most posterior extension of the suture with the pterygoid bone. The width of the palatine bone was considered to be the distance from the palatine medial border at the skull's midline to the lateral suture between the palatine and the maxilla. Table 10 summarizes these measurements for the ten genera under discussion. The ratio means column indicates that the shortest and widest bones (highest ratios) are possessed by *Chalarodon* (.846) while the longest and narrowest bones (lowest ratios) are found in *Cyclura* (.466).

TABLE 10

PALATINE BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	12.0-13.2-14.4	7.7- 8.6- 9.2	.604-.653-.721
<i>Brachylophus</i>	8.0- 8.2- 8.4	4.5- 4.9- 5.4	.560-.601-.658
<i>Chalarodon</i>	2.8- 2.8- 2.9	2.3- 2.4- 2.5	.821-.846-.862
<i>Conolophus</i>	14.2-23.1-28.4	9.1-14.4-17.7	.577-.627-.648
<i>Ctenosaura</i>	8.5-10.8-15.1	5.0- 6.0- 8.2	.543-.565-.588
<i>Cyclura</i>	12.1-20.9-30.0	6.0- 9.9-13.9	.406-.466-.502
<i>Dipsosaurus</i>	5.6- 6.4- 7.9	3.7- 4.1- 4.6	.582-.644-.678
<i>Iguana</i>	11.2-15.9-20.1	7.4- 9.1-10.6	.432-.598-.671
<i>Oplurus</i>	5.9-7.5-12.0	3.4- 3.6- 5.3	.441-.532-.576
<i>Sauromalus</i>	5.8- 9.7-12.9	3.6- 5.3- 7.0	.542-.557-.620

Premaxillae

Premaxillae (Figs. 1, 2, 3, 4, 5, and 6) is the most anterior bone of the skull, and joins the maxilla laterally and the nasal bones dorsally. It forms the rostrum of the skull.

The length of the maxillae was considered to be the distance from the anteroventral tip of the bone to its dorsal union with the nasal bones at the dorsal midline of the skull. The distances between the lateral sutures shared by the premaxilla with the maxilla on the ventral surface of the bones were considered to be the width of the premaxillae. The length and width values of the premaxilla are expressed in Table 11. The ratio mean column indicates the highest ratios (shortest, widest bones) is found in *Conolophus* (.914) while the lowest ratio (longest, narrowest bone) are found in *Cyclura* (.491), *Ctenosaura* (.512) and *Iguana* (.521).

The suture between the posterodorsal portion of

the premaxilla and the nasal bones differs from genus to genus, in the degree of penetration the premaxilla makes between the two nasal bones. In *Amblyrhynchus*, *Conolophus*, and *Iguana*, the penetration of the premaxilla is very shallow with that of *Conolophus* forming a shallow curve and penetrating the nasals very little. Deep penetrations of the premaxilla are found in *Brachylophus*, *Chalarodon* and *Oplurus*. Moderate penetrations are found in the remaining genera.

TABLE 11

PREMAXILLARY BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	10.1-12.6-14.4	6.3- 7.3- 8.2	.566-.585-.623
<i>Brachylophus</i>	7.5- 8.5- 9.8	4.2- 4.7- 5.6	.442-.558-.629
<i>Chalarodon</i>	2.5- 2.6- 2.9	1.4- 1.6- 2.0	.560-.611-.689
<i>Conolophus</i>	15.8-17.9-19.3	13.6-18.4-20.5	.860-.914-.963
<i>Ctenosaura</i>	8.0-11.0-15.0	4.1- 5.7- 8.4	.464-.512-.560
<i>Cyclura</i>	11.7-21.6-29.1	5.1-10.7-15.0	.435-.491-.566
<i>Dipsosaurus</i>	4.0- 4.9- 6.5	2.5- 3.1- 4.3	.607-.629-.661
<i>Iguana</i>	13.5-16.2-18.9	6.7- 8.4- 9.9	.485-.521-.581
<i>Oplurus</i>	4.4- 5.7- 9.1	2.5- 3.1- 5.1	.500-.542-.568
<i>Sauromalus</i>	4.7- 7.3-12.3	2.6- 4.3- 6.3	.509-.603-.676

Maxillae

Maxillae (Figs. 1, 2, 3, 4, 5 and 6) forms the major lateral surface of the snout. The ventral margin bears a single row of pleurodont teeth. There are three protrusions from the main region of the maxilla. The first protrusion is the premaxillary process which overlaps and is attached to the maxillary process of the premaxilla. The medial part of the maxillae is attached to the vomer whereas the dorsal extension forms the inferior rim of the fenestra exonarina.

The posterior process of the maxillae is attached to the jugal and lacrimal bone dorsally, and to the ectopterygoid medially. This process forms the lateral part of the rim of the inferior orbital foramen.

The third process of the maxillae extends dorsally to form the lateral wall of the nasal capsules, the posterior rim of the fenestra exonarina anteriorly, and dorsally attaches to the nasal and prefrontal bones.

The length of the maxillae was taken from the anterior most extension of the premaxillary process where it formed a suture with the premaxillae to the posterior most extension of the maxillae where it joined the jugal and ectopterygoid bones. The width of the maxillae was considered to be the vertical distance from the ventral border of the maxillae to the dorsal most extension of the bone at the point where it sutured with the nasals and prefrontals. Table 12 summarizes the maxillary measurements. The ratio mean column indicates the longest and lowest maxilla (lowest ratios) are found in *Chalarodon* (.334), *Oplurus* (.358), *Ctenosaura* (.371), *Brachylophus* (.373) and *Sauromalus* (.377). The shortest and

widest bones (highest ratio) are found in *Amblyrhynchus* (.619).

TABLE 12
MAXILLARY BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	21 7-25.3-28 8	13 5-15 4-17.5	.596-.619-.642
<i>Brachylophus</i>	15.0-17.4-18.9	6.0- 6.6- 7.5	.346-.373-.400
<i>Chalarodon</i>	6.3- 6.7- 7.2	2.2- 2.2- 2.3	.319-.334-.349
<i>Conolophus</i>	30.0-41.0-45.6	14 3-19.3-21.5	.432-.466-.483
<i>Ctenosaura</i>	16.1-21.3-29.3	5.5- 8.0-11.7	.341-.371-.399
<i>Cyclura</i>	23.4-40 6-54 3	8.9-15.5-21.4	.359-.383-.402
<i>Dipsosaurus</i>	10.1-10.8-11 9	5.0- 5.5- 6.1	.495-.513-.564
<i>Iguana</i>	27.6-35 0-40.6	11 9-13.9-15.5	.381-.399-.431
<i>Ophurus</i>	9 4-11 4-15 9	3.5- 4.1- 5.7	.346-.358-.372
<i>Sauromalus</i>	15.1-18.9-27.1	4 3- 7.2-10.8	.355-.377-.398

Nasal

Nasal (Figs. 3, 4, 5 and 6) forms the sloped top of the snout and partially covers the nasal capsule. The nasals attach posteriorly to the frontals, anteriorly to the premaxillae, and laterally to the prefrontals. Part of the anterior border of the nasal bone forms the dorsal border of the fenestra exonarina.

The measurement of length of the nasal bone was taken from the tip of the ventral border as it formed the fenestra exonarina to the posterodorsal extension that sutured with the prefrontal. Width was defined as the widest portion of the bone from its medial suture with its opposite member to the most lateral extension of the bone where it sutured with the maxilla and prefrontals. These measurements are expressed in Table 13 where the ratio mean column shows the nasals with the greatest ratio of length to width (short, wide bones) are found in *Ctenosaura* (.555) and *Brachylophus* (.522), while those with the lowest ratio (long, narrow bones) are found in *Amblyrhynchus* (.375).

The basic shape of the nasal bones differs from genus to genus. The major differences include the amount of nasal bone that borders the premaxilla, the shape of the posterior border that sutures with the frontal bone, and the shape and position of the lateral border that sutures with the maxilla and prefrontals. The nasals border a large portion of premaxilla in *Brachylophus*, *Chalarodon* and *Ophurus*. A short border with premaxilla is seen in *Amblyrhynchus*, *Conolophus* and *Iguana*. The posterior border of the nasal forms an interfingering suture with the frontal bone in *Amblyrhynchus*, *Conolophus*, *Dipsosaurus*, *Iguana*, and *Sauromalus*. The posterior projection forms a smooth suture in the remaining genera. The shape of the posterior border of the nasal bone may be roughly straight as in *Amblyrhynchus*, *Conolophus* and *Iguana* or it may form a posteriorly projecting triangle as in *Brachylophus*, *Chalarodon*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Ophurus*, and *Sauromalus*.

The lateral borders of the nasals form a shallow curve in *Brachylophus*, *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana* and *Ophurus*. In *Amblyrhynchus* and *Sauromalus* this curvature is disrupted at its anterior end by an indentation for the dorsal projection of the maxilla.

TABLE 13
NASAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	17.2-20.1-24 1	6.3- 7.5- 8.4	.348-.375-.416
<i>Brachylophus</i>	7.2- 8 7-12.4	3.9- 4.4- 5.3	.427-.522-.564
<i>Chalarodon</i>	2.3- 2.5- 2.7	1.1- 1.1- 1.3	.423-.455-.481
<i>Conolophus</i>	15 6-22.4-26 1	8.6-10 6-11.9	.409-.480-.551
<i>Ctenosaura</i>	8.1-11.5-14.8	4.2- 6.4- 8.6	.507-.555-.618
<i>Cyclura</i>	12 6-21.4-27.0	5.8-10 2-15.1	.428-.472-.559
<i>Dipsosaurus</i>	6.8- 7.2- 7.5	2.9- 3.6- 3.9	.426-.500-.541
<i>Iguana</i>	14.5-19.7-22.5	6.4- 8 9-10.5	.443-.449-.466
<i>Ophurus</i>	4.5- 5.3- 7.7	1.9- 2.4- 3.7	.422-.448-.480
<i>Sauromalus</i>	5.1- 8.8-13.0	2.5- 4.3- 6.1	.434-.496-.583

Prefrontal

Prefrontal (Figs. 3, 4, 5 and 6) forms the anterior angle of the orbit. Medially it attaches to the frontal and nasal bones, ventrally to the maxillae and posteriorly to the lacrimal.

Length measurements were taken from the suture between the prefrontal and lacrimal bones at the anterior lip of the orbit, to the suture between the prefrontal and frontal bones on the dorsal lip of the orbit. The width of the prefrontal bone was considered to be from the suture between the prefrontal and lacrimals to the medial point where the frontal, nasal, and prefrontal bones suture together as seen in Table 14. The prefrontals with the greatest ratio of length to width (shortest, widest bones) are possessed by *Amblyrhynchus* (.776). Those genera with prefrontals having the lowest ratio (long, narrow bones) include *Chalarodon* (.512) *Sauromalus* (.553), and *Brachylophus* (.571) (Table 14).

TABLE 14
PREFRONTAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	13.5-14.9-15 9	10.0-13 3-18 9	.718-.776-.849
<i>Brachylophus</i>	8 4- 9.0-10 1	4 5- 5.1- 5.8	.535-.571-.619
<i>Chalarodon</i>	2.9- 2.9- 3.1	1.5- 1 5- 1.6	.500-.512-.517
<i>Conolophus</i>	17.5-22 7-25.7	10.9-14.6-17.3	.595-.636-.676
<i>Ctenosaura</i>	8 0-10.5-13.4	5 0- 6.8- 9 1	.625-.645-.679
<i>Cyclura</i>	10 5-18 3-23.8	5.7-11.3-14.9	.542-.603-.668
<i>Dipsosaurus</i>	6 3- 6.6- 6.8	4 2- 4 3- 4.5	.656-.662-.666
<i>Iguana</i>	12 4-16.0-20.3	8.2-10.7-13.9	.621-.672-.723
<i>Ophurus</i>	4.4- 5.4- 8.0	2.8- 3.4- 5 1	.612-.636-.676
<i>Sauromalus</i>	5.3- 8.1-11 0	2.7- 4.6- 7 1	.500-.553-.645

Lacrimal

Lacrimal (Figs. 5 and 6) is a small bone on the

anteroventral rim of the orbit. Dorsally it is attached to the prefrontal, anteriorly to the maxillae, ventrally to the jugal, and ventromedially to the prefrontal.

Measurements taken on the lacrimal include length as the greatest diagonal distance from the anterodorsal border as it sutures with the prefrontal and maxilla to the posterior border on the rim of the orbit as it sutures with the jugal. Width was considered as the vertical distance between the dorsal border of the lacrimal at the rim of the orbit to the ventral border of the lacrimal at its suture with the maxilla. Those measurements summarized in Table 15 show the lowest ratio (long, narrow bones) for the lacrimal bone is found in *Chalarodon* (.293). The highest ratio (short, wide bones) is that for *Conolophus* (.542), *Ctenosaura* (.532), *Cyclura* (.526), and *Brachylophus* (.523).

In shape the lacrimal differs from genus to genus. The most common form of the bone is that of a slightly curved rhomboid. This rhomboid shape is most perfectly reproduced in *Conolophus*, *Ctenosaura*, *Cyclura* and *Iguana*. In *Amblyrhynchus* the bone is reduced to a splinterlike structure while in *Brachylophus*, *Chalarodon*, *Dipsosaurus* and *Ophurus* the rhomboid shape is distorted by the curvature of the bone to fit the rim of the orbit. In *Sauromalus* the bone has its dorsal part reduced so as to form a rough trapezoid shape.

TABLE 15
LACRIMAL BONES

Genus	Length			Width			Width-Length Ratio		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
<i>Amblyrhynchus</i>	3.2-	4.0-	5.0	1.5-	1.9-	2.7	.405-	.471-	.540
<i>Brachylophus</i>	2.4-	3.3-	4.3	1.4-	1.6-	1.9	.428-	.523-	.640
<i>Chalarodon</i>	1.0-	1.0-	1.1	0.3-	0.3-	0.3	.272-	.293-	.300
<i>Conolophus</i>	3.4-	6.1-	7.8	2.0-	3.3-	4.2	.507-	.542-	.588
<i>Ctenosaura</i>	2.4-	3.8-	6.0	1.2-	2.0-	3.3	.500-	.532-	.555
<i>Cyclura</i>	3.5-	8.3-	13.4	2.0-	4.2-	5.9	.506-	.526-	.588
<i>Dipsosaurus</i>	2.2-	2.6-	3.2	1.0-	1.0-	1.0	.312-	.392-	.454
<i>Iguana</i>	7.7-	9.4-	10.8	3.4-	4.2-	5.0	.441-	.451-	.462
<i>Ophurus</i>	1.7-	1.7-	1.8	0.6-	0.6-	0.7	.352-	.370-	.388
<i>Sauromalus</i>	2.3-	3.9-	5.7	1.0-	1.5-	1.9	.333-	.385-	.463

Septomaxilla

Septomaxilla is found within the nasal capsule where it covers Jacobson's organ and houses the anterior part of the nasal capsule. Because of the difficulty in taking measurements of this bone, it has not been studied in detail.

Frontal

Frontal (Figs. 3, 4, 5 and 6) forms the dorsal border of the orbits and the anterior roof of the braincase. At its posterior extreme the frontal is attached to the parietal and postorbital bones. Anteriorly, it is sutured to the nasal and the prefrontal. The pineal foramen penetrates the posteromedial portions of this bone or the suture it shares with the parietal.

Table 16 represents length and width measurements of the frontal bone. Length was considered to be the distance from the most anteromedial suture shared with the nasals to the most posteromedial suture shared with the parietal bone. The width of the frontal was measured as the distance between the most lateral posterior projections as they sutured with the parietal and postfrontal bones. The greatest width to length ratio (short, wide bones) is to be found in *Ctenosaura* (.936) and *Brachylophus* (.907). The smallest ratio (long, narrow bones) is that of *Amblyrhynchus* (.629).

The shape of the frontal is basically the same for all genera but differs in some small features between genera. The greatest difference in shape occurs at the anterior end where the frontal sutures with the nasals and prefrontals. In *Conolophus* the anterior border interfingers with the nasals but is essentially straight. In *Brachylophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Ophurus*, and *Sauromalus*, the anteromedial portion is triangle shaped and forms a wedge between the paired nasals. This triangle in *Dipsosaurus* is still more unique by being bifurcated at its tip by a secondary triangular projection of the nasal bones. In *Ctenosaura* and *Sauromalus* the lateral sides of the frontal's triangular projection is further bifurcated by secondary triangles. The lateral sutures of this process in *Brachylophus* interfinger with the prefrontals and nasals but is essentially straight as it is in *Cyclura*. *Amblyrhynchus* and *Chalarodon* lack this anterior traingular projection and in its place possess a depression which fits around a triangular projection formed by the posterior borders of the nasals. Thus in the latter two genera the anterior portion of the frontal bone is bifurcated and sends a projection anteriorly which serves to separate the prefrontals and nasals for a portion of their length.

The frontals of *Amblyrhynchus*, *Brachylophus*, *Conolophus* and *Cyclura* are wider than long. In the other genera the frontals are longer than wide.

The placement of the pineal foramen in the frontal bone or the suture between the frontal and parietal bones is perplexing. The foramen was found to be in

TABLE 16
FRONTAL BONES

Genus	Length			Width			Width-Length Ratio		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
<i>Amblyrhynchus</i>	12.1-	15.5-	18.1	18.9-	24.7-	30.3	.597-	.629-	.653
<i>Brachylophus</i>	11.0-	12.6-	14.2	12.6-	13.8-	14.8	.808-	.907-	.985
<i>Chalarodon</i>	5.9-	6.0-	6.2	4.8-	4.9-	5.0	.806-	.840-	.847
<i>Conolophus</i>	16.6-	21.3-	24.4	22.4-	31.2-	36.3	.631-	.689-	.746
<i>Ctenosaura</i>	11.6-	14.2-	16.6	11.1-	14.7-	18.7	.887-	.936-	.963
<i>Cyclura</i>	16.3-	22.5-	29.1	17.3-	25.8-	34.1	.839-	.886-	.942
<i>Dipsosaurus</i>	8.4-	9.5-	10.3	7.5-	8.3-	9.2	.838-	.873-	.910
<i>Iguana</i>	18.3-	21.8-	25.9	15.4-	22.1-	24.1	.806-	.894-	.946
<i>Ophurus</i>	7.3-	8.6-	12.1	6.0-	7.0-	10.0	.800-	.815-	.835
<i>Sauromalus</i>	11.0-	13.7-	18.1	9.6-	12.0-	17.4	.800-	.873-	.966

the suture between the two bones in all specimens examined of *Brachylophus*, *Chalarodon*, *Ctenosaura*, and *Iguana*. The foramen appears completely embedded in the frontal bones in one specimen each of *Amblyrhynchus*, *Conolophus*, and *Oplurus*, whereas other specimens of these genera possessed a foramen in the suture. In *Cyclura* the pineal foramen is found in the frontal bone in three of four specimens examined while it occurred in the frontal bone in all four specimens of *Dipsosaurus* and in five of six specimens of *Sauromalus*.

Postfrontal

Postfrontal (Figs. 3, 4, 5 and 6) forms a small part of the posterodorsal margin of the orbit. Posteriorly this bone is sutured to the frontal, and laterally to the postorbital and the parietal.

The length of the postfrontal was measured as the distance between the extremities of its longest axis. The width was the distance between the parallel borders on the axis at right angles to the length. The values for these measurements are presented in Table 17 and it can be seen that the genus with the smallest ratio (longest, narrowest bone) is *Chalarodon* (.200), while *Oplurus* (.625) has the largest ratio (shortest, widest bones).

The postfrontal is usually splinterlike in shape as it is in all genera except *Cyclura*, *Iguana* and *Oplurus*. In *Cyclura* the anterolateral portion of the bone forms a short projection out over the posterodorsal part of the orbit in some individuals. This condition is especially well developed in *Cyclura cornuta*. In *Iguana* the lateral portions of the postfrontal is developed into a prominent knob on the anterodorsal face of the postorbital bone. In *Oplurus* the postfrontal is small, almost spherical in shape, and in at least one skull (MCZ 37191) this bone could not be located.

TABLE 17
POSTFRONTAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	6.9- 8.7-10.3	3.8- 4.2- 4.6	.436-.489- .550
<i>Brachylophus</i>	4.0- 4.7- 6.2	1.1- 1.3- 1.8	.275-.286- .300
<i>Chalarodon</i>	0.5- 0.5- 0.5	0.1- 0.1- 0.1	.200-.200- .200
<i>Conolophus</i>	10.0-13.6-16.7	2.3- 3.5- 4.4	.230-.256- .269
<i>Ctenosaura</i>	3.9- 4.8- 5.8	0.8- 1.1- 1.7	.207-.234- .293
<i>Cyclura</i>	6.5- 9.4-12.4	1.9- 2.7- 3.9	.219-.287- .326
<i>Dipsosaurus</i>	2.4- 2.7- 3.0	0.5- 0.6- 0.8	.204-.235- .266
<i>Iguana</i>	4.6- 7.0- 8.4	2.0- 2.7- 3.2	.360-.394- .434
<i>Oplurus</i>	0.2- 0.2- 0.3	0.1- 0.1- 0.3	.500-.625-1.000
<i>Sauromalus</i>	2.1- 3.8- 5.6	0.7- 1.3- 1.9	.310-.380- .388

Jugal

Jugal (Figs. 1, 2, 3, 4, 5 and 6) forms the ventral border of the orbit and a small part of the supratemporal arch. Anteriorly it attaches to the maxillae, ventrally to the lacrimal and palatine bones, and medially

to the ectopterygoid. The dorsal surface forms the anteroventral wall of the orbit.

The length of the jugal is considered as the horizontal distance between the most anterior projections of the bone as it sutured to the lacrimal and maxillae, to the most posterior projection which sutured to the anteroventral border of the postorbital. The width was the widest distance between the two parallel borders at right angles to the length. Measurements of the jugal bones are presented in Table 18. The smallest ratio (longest, narrowest bone) of length to width is found in *Ctenosaura* (.136), *Sauromalus* (.141), and *Oplurus* (.148). The largest ratios (shortest, widest bones) are found in *Amblyrhynchus* (.207), *Conolophus* (.195), and *Cyclura* (.191).

The posterior extension of the jugal may extend so far posteriorly as to touch or overlap the squamosal, thereby completely covering the ventral border of the postorbital bone. Such a condition exists in *Conolophus*, *Dipsosaurus*, *Iguana*, and *Oplurus*. In the other genera the jugals and squamosals do not touch.

TABLE 18
JUGAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	18.1-21.0-24.7	3.4- 4.3- 5.2	.169-.207-.236
<i>Brachylophus</i>	12.5-13.7-15.9	2.0- 2.7- 3.5	.160-.172-.220
<i>Chalarodon</i>	6.1- 6.4- 6.8	1.0- 1.1- 1.2	.163-.169-.176
<i>Conolophus</i>	26.2-34.2-38.2	5.4- 6.6- 7.2	.188-.195-.206
<i>Ctenosaura</i>	14.0-19.2-27.3	1.6- 2.6- 3.7	.114-.136-.155
<i>Cyclura</i>	24.0-38.5-50.8	3.1- 7.7-11.8	.129-.191-.265
<i>Dipsosaurus</i>	11.6-12.1-12.8	1.7- 1.9- 2.2	.141-.161-.180
<i>Iguana</i>	20.0-26.8-31.9	3.2- 4.2- 5.0	.141-.156- .167
<i>Oplurus</i>	9.4-10.7-13.9	1.3- 1.6- 2.1	.139-.148-.159
<i>Sauromalus</i>	11.9-15.9-24.1	1.3- 2.4- 3.4	.109-.141- .196

Parietal

Parietal (Figs. 3, 4, 5 and 6) forms the roof of the posterior part of the skull. It articulates with the frontal and postfrontal anteriorly and with the postorbital posteriorly and ventrally. Posteriorly the parietal overlays the supratemporal and articulates with the exoccipitals and supraoccipital.

The anterior two thirds of the dorsal surface of the parietal gives origin to the pseudotemporalis superficialis muscle, and the posterior one-third gives origin to the adductor externus medius. The posterior tip of the supratemporal process supplies the origin for a part of the adductor externus profundus muscle. Laterally the parietal bone gives origin to the levator pterygoideus. The posterior border of the parietal provides attachment to the origin of the depressor mandibularis and the insertion of the spinus dorsi, longissimus dorsi, and episternocleidomastoideus muscles.

Measurements were taken of two areas of the parietal bone. The anterior two-thirds of the bone was

subjected to length-width measurements, with the length being the distance along the midline, from the anterior suture with the frontal to the suture between the parietal and the supraoccipital. The width of the parietal was considered as the distance between the two most anterolateral projections of the bone where they sutured with the postorbital and postfrontals. The measurements are presented in Table 19. The greatest length width ratio (shortest, widest bone) is found in *Conolophus* (.751) while *Dipsosaurus* (.431), and *Brachylophus* (.448) possess the smallest ratio (longest, narrowest bones).

The second portion of the parietal to be measured was the wings or posterior dorsolateral projections of the bone that sutured with the supratemporal, squamosal, and articulated with the quadrate. The length of the parietal wings is the diagonal distance from the anterolateral portion of the parietal bone to the opposite posterior tip of the parietal wing. The width is the distance between the most posterolateral surface of the two wings. The parietal wing ratios are summarized in Table 20 and show the greatest length width ratios (shortest, widest bones) to be possessed by *Dipsosaurus* (.945) and *Sauromalus* (.926). The lowest ratios (longest, narrowest bones) are those of *Brachylophus* (.765) and *Ctenosaura* (.781).

Supratemporal

Supratemporal provides support for the postero-

lateral angle of the parietal bone. Posteriorly, it articulates with the exoccipital, squamosal, and the quadrate.

On the medial border of the anterior part is a partial origin for the adductor mandibularis externus profundus muscle and on the lateral border is the origin of the adductor mandibularis externus medius muscle. Because of the difficulties in measuring, this bone has not been studied in detail.

Postorbital

Postorbital (Figs. 1, 2, 3, 4, 5 and 6) forms part of the posterior rim of the orbit. The dorsal part is sutured anteriorly to the postfrontal and posteriorly to the parietal bone. The anteroventral border articulates with the jugal and the posteroventral border of the squamosal.

The ventral free border of the postorbital gives origin to the anterior half of the levator angularis oris muscle, whereas the medial surface of the posterior half gives origin to the adductor mandibularis externus superficialis muscle.

The length of the postorbital was measured as the greatest distance between anteroventral and posteroventral projections. The width was considered as the distance from the ventral border to the tip of the dorsal projection where it sutured with the parietal and postfrontal bones. Table 21 shows that the greatest length width ratio (shortest, widest bones) is found in *Iguana* (.886), *Amblyrhynchus* (.882), and *Conolophus* (.876). The lowest ratio (longest, narrowest bones) is possessed by *Sauromalus* (.556) and *Cyclura* (.585).

The postorbital bone is roughly triangular in shape in all genera. Its ventral border has been discussed in the description of the jugal. This border is completely covered by the squamosal and jugal bones in *Conolophus*, *Dipsosaurus*, *Iguana*, and *Oplurus*. In the other genera the central part of the ventral border is free. In *Amblyrhynchus* the anterior face of the dorsal process is enlarged and contributes to the knoblike structure of the postfrontal. The postorbital of *Cyclura* appears normal and does not contribute to the postfrontal knob over the orbit.

TABLE 19
PARIETAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	9.9-12.2-16.1	19.4-24.2-29.2	.444-.502-.551
<i>Brachylophus</i>	5.9- 6.5- 7.4	12.8-14.7-18.7	.395-.448-.496
<i>Chalarodon</i>	2.6- 2.8- 3.1	4.9- 5.2- 5.5	.530-.550-.563
<i>Conolophus</i>	16.3-24.9-29.3	24.7-32.5-37.1	.659-.751-.789
<i>Ctenosaura</i>	7.1- 9.0-11.0	11.6-13.4-21.0	.522-.552-.612
<i>Cyclura</i>	10.3-19.2-32.9	18.1-28.8-41.7	.515-.640-.788
<i>Dipsosaurus</i>	3.4- 3.9- 4.3	8.1- 9.1- 9.7	.419-.431-.443
<i>Iguana</i>	10.9-12.8-14.7	18.4-21.8-24.5	.566-.585-.600
<i>Oplurus</i>	3.9- 4.4- 5.5	7.8- 8.7-11.3	.486-.510-.555
<i>Sauromalus</i>	5.0- 7.6-10.0	10.1-13.2-19.3	.495-.566-.646

TABLE 20
PARIETAL WINGS

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	28.1-33.1-38.1	24.4-29.1-33.5	.868-.878-.891
<i>Brachylophus</i>	13.4-14.3-16.1	17.3-18.3-20.5	.734-.765-.785
<i>Chalarodon</i>	7.0- 7.4- 7.7	6.3- 6.5- 6.7	.840-.880-.957
<i>Conolophus</i>	34.1-50.8-58.5	27.4-40.6-48.4	.771-.802-.827
<i>Ctenosaura</i>	15.7-25.4-30.9	12.5-18.9-25.8	.747-.781-.802
<i>Cyclura</i>	25.0-42.4-58.1	19.3-35.0-48.8	.772-.817-.839
<i>Dipsosaurus</i>	12.6-13.6-14.4	12.4-12.8-13.2	.916-.945-.984
<i>Iguana</i>	23.2-29.3-33.4	19.6-25.5-28.7	.814-.870-.925
<i>Oplurus</i>	11.0-12.7-18.0	9.0-10.5-15.1	.810-.824-.833
<i>Sauromalus</i>	12.9-19.7-29.0	11.9-19.1-28.0	.897-.926-.980

TABLE 21
POSTORBITAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	9.1-13.5-17.5	8.5-11.8-15.3	.850-.882-.934
<i>Brachylophus</i>	5.5- 6.4- 7.8	4.1- 4.9- 6.0	.745-.771-.800
<i>Chalarodon</i>	3.1- 3.3- 3.7	2.4- 2.4- 2.6	.702-.734-.774
<i>Conolophus</i>	16.0-25.7-30.4	14.3-23.1-27.4	.824-.876-.901
<i>Ctenosaura</i>	8.0-11.3-15.0	4.2- 6.9- 9.1	.525-.607-.690
<i>Cyclura</i>	14.0-22.1-35.3	7.5-15.2-21.6	.535-.585-.614
<i>Dipsosaurus</i>	5.4- 6.4- 7.1	4.0- 4.9- 5.9	.740-.789-.835
<i>Iguana</i>	9.8-14.1-16.7	9.0-12.4-15.4	.842-.886-.922
<i>Oplurus</i>	5.0- 5.8- 8.2	3.6- 4.3- 5.9	.704-.719-.760
<i>Sauromalus</i>	7.3-10.0-15.5	3.7- 5.7- 9.2	.500-.556-.605

Squamosal

Squamosal (Figs. 1, 2, 3, 4, 5 and 6) is attached to the postorbital bone on the posterolateral border of the skull. The expanded posterior part of the squamosal is attached to the dorsal surface of the supratemporal and the quadrate.

The lateral surface of the squamosal provides an area of origin for the adductor mandibularis externus superficialis and part of the levator angularis oris muscle. The medial surface gives origin to the adductor mandibularis externus medius muscle.

The length of the squamosal was measured as the distance between the most anterior and the posterior extremities of the bone. The width was the greatest distance between the parallel borders on an axis at right angles to the length. These measurements are presented in table 22 and show the greatest ratio (shortest, widest bones) to be found in *Amblyrhynchus* (.736). The smallest ratio (longest, narrowest bones) occurs in *Chalarodon* (.063).

The shape of the squamosal bone differs not only in size but in shape as well. The posterior projection of the bone has a dorsal and ventral hooklike projection in *Chalarodon* and *Ophurus*. Those of *Ophurus* are not as pronounced as those in *Chalarodon*. The posterior portion of the bone in other genera is swollen but the projections are in the forms of small triangular processes rather than curving hooks as in *Chalarodon* and *Ophurus*. The greatest development of these triangular projections is found in *Amblyrhynchus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Iguana*, and *Sauromalus*. The squamosals take the form of a long split in *Dipsosaurus* and *Brachylophus*.

TABLE 22
SQUAMOSAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	7.1-10.2-12.9	5.7- 7.4- 9.5	.606-.736-.802
<i>Brachylophus</i>	6.1- 7.1- 8.5	2.0- 2.2- 2.6	.280-.304-.327
<i>Chalarodon</i>	3.0- 3.1- 3.5	0.2- 0.2- 0.2	.057-.063-.066
<i>Conolophus</i>	13.0-20.6-24.3	5.2-10.0-13.4	.400-.476-.551
<i>Ctenosaura</i>	5.9- 9.1-13.0	1.3- 2.6- 5.2	.202-.234-.268
<i>Cyclura</i>	9.8-18.1-23.1	2.4- 4.9- 8.0	.244-.297-.346
<i>Dipsosaurus</i>	6.0- 6.4- 7.1	1.5- 1.5- 1.7	.245-.268-.309
<i>Iguana</i>	9.8-11.2-12.2	3.0- 4.1- 5.0	.306-.369-.434
<i>Ophurus</i>	4.1- 5.4- 8.6	1.3- 1.5- 2.2	.244-.296-.369
<i>Sauromalus</i>	4.6- 7.9-10.1	1.0- 2.4- 4.3	.217-.299-.373

Quadrate

Quadrate (Figs. 1, 2, 3, 4, 5 and 6) is found at the posterolateral angle of the skull where it provides the articulating area between skull and lower jaw. It also forms the seat of the middle ear and attachment for the adductor musculature and tympanic membrane.

Mesially the quadrate is attached to the parietal, dorsally to the snratemporal, and laterally to the squamosal bone. Other parts of its dorsal surface

provide for the origin of the adductor mandibularis superficialis muscles. The medial half and its crest serve as origin for the adductor mandibularis posterior muscle. The posterior end of this area attaches to the prootic bone and the quadrate process of the pterygoid.

The tympanic crest serves as a place of attachment for the tympanic membrane and the origin of the adductor mandibularis externus superficialis muscle.

The length of the quadrate is the distance from the dorsal border of the bone where it attaches to the squamosal and the ventral extremity of the condyle of articulation with the articular bone of the lower jaw. Width is the greatest distance between medial and lateral borders of the bone. Table 23 summarizes the quadrate measurements. Quadrates with the greatest length-width ratios (shortest, widest bones) are found in *Sauromalus* (.737). The smallest quadrate ratio (longest, narrowest bone) is that of *Dipsosaurus* (.531), *Iguana* (.537), and *Brachylophus* (.546).

TABLE 23
QUADRATE BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	9.8-11.6-13.5	7.0- 8.0- 9.3	.614-.690-.718
<i>Brachylophus</i>	7.0- 7.4- 8.0	4.1- 4.3- 4.5	.537-.549-.642
<i>Chalarodon</i>	2.7- 2.9- 3.2	1.8- 1.8- 1.9	.593-.628-.666
<i>Conolophus</i>	13.4-19.7-24.9	8.3-13.7-17.0	.619-.693-.774
<i>Ctenosaura</i>	7.0- 8.9-11.0	4.4- 5.8- 8.1	.625-.653-.736
<i>Cyclura</i>	10.0-17.9-24.2	5.0- 8.9-15.0	.500-.557-.615
<i>Dipsosaurus</i>	6.0- 6.2- 6.8	3.1- 3.3- 3.7	.516-.531-.544
<i>Iguana</i>	10.5-12.7-13.6	4.9- 6.9- 7.9	.457-.537-.580
<i>Ophurus</i>	4.0- 4.7- 6.7	2.4- 3.1- 4.1	.600-.662-.731
<i>Sauromalus</i>	5.0- 7.0-10.0	3.2- 5.2- 7.1	.640-.737-.887

Epipterygoid

Epipterygoid extends between the parietal and the pterygoid. Its dorsal tip appears to be held in place by the origin of the pseudotemporalis superficialis muscle. The upper one-third of this bone serves as the origin for the pseudotemporalis superficialis muscle. The ventral two-thirds serves as origin for the pseudotemporalis profundus muscle. This bone was not studied in detail.

Supratemporal fossa

Supratemporal fossa (Figs. 3 and 4) is the large cavity that dominates each half of the dorsal posterior third of the skull. It is bordered medially, posteromedially, and anteromedially by the parietal bone, anterolaterally by the postorbital, and posterolaterally by the squamosal.

Length and width measurements were taken of the supratemporal fossa, with length being the inside distance on the longest axis and width being the inside distance on the longest axis at right angles to the length. Table 24 shows the largest length-width ratios

(shortest, widest opening) are possessed by *Dipsosaurus* (.647), *Sauromalus* (.620), *Amblyrhynchus* (.616), and *Conolophus* (.609). The smallest ratio (longest, narrowest opening) is found in *Chalarodon* (.443).

TABLE 24
SUPRATEMPORAL FOSSA

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	12.5-15.2-18.3	6.3- 9.4-11.9	.504-.616-.781
<i>Brachylophus</i>	8.0- 9.4-12.1	4.3- 5.4- 6.9	.514-.577-.637
<i>Chalarodon</i>	3.4- 3.6- 4.3	1.5- 1.6- 1.9	.428-.443-.462
<i>Conolophus</i>	18.0-28.8-34.0	12.0-17.4-21.2	.560-.609-.666
<i>Ctenosaura</i>	8.1-11.0-13.9	4.9- 8.8- 9.1	.589-.615-.654
<i>Cyclura</i>	12.0-21.2-28.0	5.1-11.3-19.1	.425-.515-.682
<i>Dipsosaurus</i>	4.2- 5.0- 5.7	2.6- 3.2- 3.7	.619-.647-.687
<i>Iguana</i>	10.9-14.2-16.8	4.6- 7.1- 8.3	.422-.499-.567
<i>Oplurus</i>	4.2- 5.3- 8.0	2.1- 2.8- 4.1	.500-.524-.586
<i>Sauromalus</i>	5.0- 8.0-12.6	2.4- 5.0- 8.1	.480-.620-.672

Orbit

Orbit (Figs. 3 and 4) is the dominate lateral cavity of the skull and in life is the area where the eye is located. The orbit is basically circular and is bordered dorsally by the frontal; anteriorly by the prefrontals, lacrimals and jugals, ventrally by the jugal and posteriorly by the postorbital and the postfrontal.

The length of the orbit was measured as the greatest distance between lacrimal and postorbital. The width was the greatest distance between jugal and frontal bones. These relationships are expressed in Table 25 which shows the greatest length-width ratios (most circular opening) to be found in *Conolophus* (.969) and the smallest ratio (most elliptical opening) in *Chalarodon* (.682).

TABLE 25
ORBIT

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	12.4-14.3-16.3	10.9-15.8-19.5	.802-.827-.866
<i>Brachylophus</i>	11.3-11.9-13.2	9.0- 9.7-10.9	.796-.811-.825
<i>Chalarodon</i>	5.2- 6.2- 7.3	3.9- 4.2- 4.5	.611-.682-.769
<i>Conolophus</i>	17.8-23.9-26.6	17.2-23.3-26.9	.958-.969-.988
<i>Ctenosaura</i>	12.1-15.3-18.3	7.6-12.0-14.1	.770-.782-.793
<i>Cyclura</i>	16.8-25.6-33.1	12.8-20.7-27.5	.760-.803-.830
<i>Dipsosaurus</i>	8.6- 9.5-10.1	7.0- 7.5- 7.9	.770-.790-.813
<i>Iguana</i>	19.0-21.3-24.9	15.3-17.5-19.3	.775-.825-.867
<i>Oplurus</i>	7.6- 8.3-12.1	5.9- 7.0- 9.2	.760-.795-.839
<i>Sauromalus</i>	9.6-13.1-17.9	7.1- 9.9-13.5	.711-.741-.776

Fenestra exonarina

Fenestra exonarina (Figs. 3, 4, 5 and 6) is the paired prominent opening on the dorsal rostrum of the skull. It is bordered medially and anteroventrally by the premaxilla, laterally by the maxilla, and posterodorsally by the nasals. In life the fenestra

exonarina provides the opening for the external nares.

The length of the fenestra exonarina was considered to be the internal distance between the suture of the lateral projection of the premaxilla and the maxilla and the suture between the nasal and maxilla. The width was considered to be the greatest inside distance between the lateral border of the premaxilla and the anterior border of the maxilla. Table 26 represents a tabulation of these values and shows the greatest ratio (most circular opening) to exist in *Brachylophus* (.872) and the lowest ratio (most elliptical opening) to be found in *Cyclura* (.443).

The lower jaw consists of two paired rami which unite anteriorly in a mental symphysis and each articulates with the quadrate of the skull posteriorly. The dentary of each ramus bears a single row of pleurodont teeth, whereas the remaining bones (articular, surangular, angular, splenial and coronoid) are edentate.

TABLE 26
FENESTRA EXONARINA

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	8.1- 9.1-10.3	5.8- 7.0- 8.0	.716-.764-.817
<i>Brachylophus</i>	4.0- 4.2- 4.8	3.3- 3.7- 4.0	.804-.872-.951
<i>Chalarodon</i>	1.4- 1.5- 1.8	1.0- 1.0- 1.1	.611-.664-.714
<i>Conolophus</i>	11.7-15.4-17.5	8.5-11.9-13.6	.726-.767-.803
<i>Ctenosaura</i>	4.1- 5.5- 6.8	3.0- 4.1- 5.0	.700-.743-.806
<i>Cyclura</i>	7.3-20.4-32.1	5.3- 9.0-14.5	.428-.443-.452
<i>Dipsosaurus</i>	3.2- 3.8- 4.2	2.0- 2.3- 2.5	.571-.590-.606
<i>Iguana</i>	8.2-11.7-14.3	5.5- 7.8- 8.7	.608-.669-.714
<i>Oplurus</i>	1.9- 2.5- 4.2	1.4- 1.8- 3.1	.700-.718-.738
<i>Sauromalus</i>	3.0- 4.6- 6.8	2.1- 4.1- 5.0	.600-.751-.833

Dentary

Dentary (Figs. 5, 6 and 7) is the largest bone of the lower jaw and bears teeth on its dorsomedial border. At its posterior margins the dentary interdigitates with the coronoid, splenial, angular, articular, and surangular. The ventral border provides the origin for the anterior fibers of the mandibulo-hyoideus I and III and the genioglossus muscles.

Measurements taken on the dentary included the length as the distance from the anterior tip of the bone to the posterior most projection on the lateral surface of the mandible. The width of the dentary was that vertical distance between the top and the bottom of the mandible immediately in front of the coronoid. An examination of Table 27 reveals that the largest length-width ratio (smallest, widest bone) for the dentary is possessed by *Amblyrhynchus* (.297) and *Conolophus* (.282). The smallest ratio (longest, narrowest bone) is that of *Oplurus* (.147) and *Chalarodon* (.174).

The relationship between the posterolateral border of the dentary, the coronoid and the surangular differs from genus to genus. In *Chalarodon* and

Ophurus the dentary is not overlapped by the coronoid on its posterodorsal surface. In *Brachylophus*, *Ctenosaura*, *Dipsosaurus*, *Iguana* and *Sauromalus*, the dentary is overlapped dorsally by the coronoid and the ventral border of the coronoid and its suture with the dentary is parallel to the ventral border of the mandible. The posterior suture of the dentary in *Brachylophus*, *Ctenosaura*, *Iguana* and *Sauromalus* is concave in nature. In *Dipsosaurus* this suture is convex. *Amblyrhynchus*, *Conolophus* and *Cychura* have complex rounded or slanting suture between the ventral border of the overlapping coronoid and its suture with the dentary. The posterolateral suture in these genera is complex with two posteriorly pointing triangular projections being present in *Amblyrhynchus* and *Conolophus*. *Cychura* possesses a smooth gently curving concave suture.

TABLE 27
DENTARY BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	20.3-28.3-34.3	7.5- 8.3-10.2	.271-.297-.320
<i>Brachylophus</i>	19.8-21.4-23.1	4.0- 4.5- 5.0	.202-.209-.216
<i>Chalarodon</i>	8.1- 9.2-10.0	1.3- 1.5- 2.0	.142-.174-.209
<i>Conolophus</i>	40.4-51.2-55.6	8.7-14.7-17.4	.215-.282-.319
<i>Ctenosaura</i>	19.2-26.7-35.6	3.4- 5.2- 7.5	.171-.190-.210
<i>Cychura</i>	29.5-51.3-72.3	6.5-10.9-15.0	.202-.214-.228
<i>Dipsosaurus</i>	12.9-14.7-15.9	3.1- 3.6- 3.9	.240-.243-.246
<i>Iguana</i>	30.0-40.3-47.5	6.7- 9.3-10.8	.213-.225-.239
<i>Ophurus</i>	13.2-17.1-24.0	2.1- 2.4- 3.1	.129-.147-.159
<i>Sauromalus</i>	13.6-20.0-28.4	2.5- 3.6- 5.5	.143-.181-.203

Articular

Articular (Figs. 5, 6 and 7) is that part of the mandibles which articulates with the quadrate of the skull. This bone with its retroarticular process serves as the point for insertion for the depressor mandibularis, intermandibularis posterior, fibers of the pterygomandibularis, and adductor mandibularis externus muscles. The medial border is sutured to the splenial bone.

The length of the articular bone was measured from its most anterior projection on the medial surface where it sutured to the coronoid and splenial to the most posterior tip of the retroarticular process. The width was taken from the most ventromedial projection of the angular process to the opposite border of the articular bone where it sutured with the surangular on the mandible's lateral surface. These measurements are summarized in Table 28 which shows the greatest length-width ratio (shortest, widest bones) to be found in *Conolophus* (.390) and the lowest ratio is possessed by *Chalarodon* (.200).

The angular process of the articular bone differs in shape and size from genus to genus. This projection was also subjected to length-width measurements. The length was taken as the greatest length of the

mandible and was contrasted with the width of the articular which in part is a result of the size of the angular process. The ratio between those measurements is expressed in Table 29 which shows *Conolophus* (.219) to have the greatest ratio (shortest, widest bones), while the smallest ratios (longest, narrowest bones) are those of *Chalarodon* (.105) and *Ophurus* (.120).

As previously indicated, the shape of the angular process (Figure 7) differs from genus to genus. The projection which extends medially from the posterior ventromedial surface of the articular bone is either a small rounded bump as in *Amblyrhynchus* and *Iguana*, or a pointed spinelike anteriorly pointing projection as in the remaining genera. The smallest projection is that of *Amblyrhynchus*. Of the pointed projections, that of *Cychura* is the most massive and pronounced, whereas the projection in *Conolophus* is nearly as large. The angular process of *Ctenosaura* and *Sauromalus* is less massive and projecting than that of *Cychura* and *Conolophus*. It is similar in shape but less pointed in the last two genera. In *Brachylophus*, *Chalarodon*, *Dipsosaurus* and *Ophurus*, the angular projection is more triangular shaped than hooklike. In all four genera the anterior face terminates as a sharp spine. The process of *Brachylophus* and *Ophurus* is more sharply curved and hooklike than that of *Chalarodon* and *Dipsosaurus*.

TABLE 28
ARTICULAR BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	18.4-25.0-30.0	5.9- 8.1-10.8	.258-.320-.360
<i>Brachylophus</i>	16.0-17.4-18.4	4.3- 5.3- 6.4	.240-.309-.400
<i>Chalarodon</i>	6.1- 6.3- 6.7	1.2- 1.2- 1.4	.193-.200-.208
<i>Conolophus</i>	34.2-52.8-61.5	11.7-21.1-27.2	.342-.394-.457
<i>Ctenosaura</i>	14.1-21.4-21.2	4.6- 6.4-10.6	.238-.297-.340
<i>Cychura</i>	24.2-42.4-57.8	4.7-12.0-20.3	.182-.264-.351
<i>Dipsosaurus</i>	8.9-11.3-12.6	3.0- 3.6- 4.1	.298-.320-.337
<i>Iguana</i>	23.4-31.9-38.7	7.4- 8.6- 9.1	.227-.271-.316
<i>Ophurus</i>	8.3-11.3-15.8	1.9- 3.0- 4.9	.228-.257-.310
<i>Sauromalus</i>	14.8-20.7-25.5	2.8- 5.5- 9.3	.185-.253-.325

TABLE 29
ANGULAR PROCESS

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	35.0-48.4- 57.1	6.4- 9.5-11.5	.182-.196-.203
<i>Brachylophus</i>	32.2-33.6- 35.6	4.2- 5.4- 6.6	.130-.157-.185
<i>Chalarodon</i>	12.0-12.6- 13.4	1.0- 1.3- 1.8	.081-.105-.134
<i>Conolophus</i>	66.6-95.1-107.6	11.6-21.3-27.2	.174-.219-.256
<i>Ctenosaura</i>	30.2-43.1- 60.4	3.9- 6.3-10.6	.123-.141-.174
<i>Cychura</i>	48.7-84.7-117.3	7.9-14.5-21.1	.162-.169-.179
<i>Dipsosaurus</i>	19.9-23.2- 25.4	3.5- 4.1- 4.4	.169-.174-.175
<i>Iguana</i>	50.0-65.4- 77.2	7.5- 8.6- 9.2	.112-.134-.150
<i>Ophurus</i>	18.2-24.3-34.7	1.9- 3.0- 4.9	.104-.120-.141
<i>Sauromalus</i>	22.4-33.4-43.1	2.8- 5.5- 9.3	.113-.138-.167

Surangular

Surangular (Figs. 5, 6 and 7) forms the lateral wall of the posterior third of mandible. The dorsal border serves as the area of insertion for the adductor mandibularis externus muscle, and the intermandibularis posterior muscle inserts on its lateral surface.

The surangular's length is taken as the longest anterior-posterior axis on the lateral surface of the mandible. The width is considered to be the longest dorsal-ventral axis in the area of the anterior sutures with the dentary and coronoid on the mandible's lateral surface. Table 30 indicates the largest length-width ratio (shortest, widest bone) is found in *Amblyrhynchus* (.425) and the smallest ratio (longest, narrowest bone) in *Sauromalus* (.270) and *Iguana* (.278).

TABLE 30
SURANGULAR BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	11.9-16.6-21.6	5.8- 6.9- 8.9	.365-.425-.487
<i>Brachylophus</i>	9.2- 9.6-10.4	3.4- 3.6- 3.9	.369-.377-.389
<i>Chalarodon</i>	2.9- 2.9- 3.1	1.0- 1.0- 1.1	.344-.352-.366
<i>Conolophus</i>	25.5-45.3-62.1	9.0-15.2-18.0	.289-.343-.365
<i>Ctenosaura</i>	11.4-16.8-25.4	3.1- 4.7- 6.6	.271-.296-.309
<i>Cyclura</i>	20.1-24.0-44.3	5.0-10.2-15.1	.248-.296-.340
<i>Dipsosaurus</i>	6.5- 7.7- 8.7	2.4- 2.7- 3.0	.344-.356-.369
<i>Iguana</i>	20.0-25.2-30.4	5.4- 7.0- 8.5	.270-.278-.299
<i>Oplurus</i>	5.0- 6.1- 8.2	1.4- 1.8- 2.6	.280-.293-.316
<i>Sauromalus</i>	8.8-13.3-19.6	2.1- 3.6- 6.0	.229-.270-.306

Splénial

Splénial (Fig. 7) is found on the mesial side of the jaw where it connects with the angular, articular, surangular, dentary, and coronoid bones. The intermandibularis anterior profundus muscle has its origin on this bone.

The splénial's length was considered to be the longest anterior-posterior axis and the longest dorsal-ventral axis was taken as the width. Table 31 indicates the largest ratio (shortest, widest bone) is found in *Chalarodon* (.405) and the smallest ratio (longest, narrowest bone) is that of *Cyclura* (.149).

The splénial bone is a fusiform splinter shape in all ten genera but it is pierced by the anterior inferior alveolar foramen in different places in different genera. This foramen is completely enclosed within the bone in *Amblyrhynchus* and *Oplurus*. In *Brachylophus* the anterior tip of the bone forms the posterior border of the foramen. In *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Iguana* and *Sauromalus*, the foramen is partially enclosed by the anterodorsal border of the splénial. In *Dipsosaurus* the foramen is found in the dentary and is separated from the splénial by a projection of the coronoid.

Angular

Angular (Figs. 5, 6 and 7) is a flat bone whose

TABLE 31
SPLENIAL BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	8.0-10.8-14.3	2.1- 3.1- 4.1	.230-.296-.425
<i>Brachylophus</i>	6.5- 6.8- 7.2	2.0- 2.4- 3.4	.263-.361-.513
<i>Chalarodon</i>	4.3- 4.3- 4.5	1.7- 1.7- 1.9	.395-.405-.422
<i>Conolophus</i>	13.4-20.0-24.4	4.2- 6.3- 7.9	.252-.317-.393
<i>Ctenosaura</i>	7.7- 9.7-12.4	1.3- 2.2- 3.0	.186-.230-.300
<i>Cyclura</i>	12.0-21.8-30.0	1.9- 3.3- 5.3	.120-.149-.176
<i>Dipsosaurus</i>	3.7- 4.4- 5.3	1.3- 1.4- 1.7	.283-.334-.378
<i>Iguana</i>	14.7-20.6-24.6	4.7- 6.2- 7.7	.255-.301-.319
<i>Oplurus</i>	8.4-10.9-15.3	1.5- 1.8- 2.4	.156-.166-.178
<i>Sauromalus</i>	5.0- 9.0-12.1	1.0- 1.8- 2.8	.151-.199-.231

posterior part forms the ventral surface of the jaw between the articular and surangular. The anterior process of the angular attaches to the dentary. Part of this bone serves as the origin for the mandibulo-hyoideus I muscle.

The angular is roughly fusiform and its length was measured between the most anterior and most posterior projections. The width was the greatest distance between the opposite borders on an axis at right angles to the length. These measurements are summarized in Table 32 which indicates the greatest ratio (shortest, widest bone) to be that of *Dipsosaurus* (.223) and the shortest ratio (longest, narrowest bone) to be *Sauromalus* (.107).

TABLE 32
ANGULAR BONES

Genus	Length	Width	Width-Length Ratio
	Min. Mean Max.	Min. Mean Max.	Min. Mean Max.
<i>Amblyrhynchus</i>	12.4-16.4-19.5	2.8- 3.5- 4.1	.202-.214-.225
<i>Brachylophus</i>	9.2-10.5-12.1	1.4- 2.0- 2.5	.152-.189-.211
<i>Chalarodon</i>	3.0- 3.5- 4.4	0.5- 0.5- 0.7	.156-.160-.166
<i>Conolophus</i>	24.1-37.4-46.7	4.9- 7.1- 8.8	.155-.193-.226
<i>Ctenosaura</i>	10.2-16.5-23.1	2.1- 2.7- 3.3	.134-.171-.204
<i>Cyclura</i>	16.4-31.8-43.1	2.5- 4.3- 5.6	.129-.139-.152
<i>Dipsosaurus</i>	7.6- 8.0- 8.3	1.6- 1.8- 1.9	.227-.223-.230
<i>Iguana</i>	19.2-24.5-30.4	3.2- 4.1- 4.8	.157-.170-.193
<i>Oplurus</i>	4.7- 6.1- 9.4	0.9- 1.1- 1.5	.159-.189-.204
<i>Sauromalus</i>	6.5-10.1-14.5	0.5- 1.3- 2.4	.076-.107-.165

Coronoid

Coronoid (Figs. 5, 6 and 7) straddles the other bones of the jaw from a dorsal position. The two anterior extremities articulate in most genera with the dentary and surangular laterally and the dentary, splénial and articular bone ventrally.

The posterior, lateral, apical surfaces give rise to the insertion of the adductor mandibularis externus and adductor medius muscles, and provides an attachment surface for the bodenaponeurosis.

The coronoid length was measured as the distance from the dorsal tip of the bone to the tip of the ventral most projection on the lateral surface of the

mandible. The width was the distance between anterior and posterior borders where they contact the dorsolateral surface of the mandible. Table 33 shows the greatest ratio (shortest, widest bones) is found in *Chalarodon* (.941) and *Amblyrhynchus* (.935). The lowest ratio (longest, narrowest bones) is that of *Conolophus* (.571).

The shape of the bone differs greatly from genus to genus. The anterolateral projection of the coronoid takes different shapes in different genera. In *Chalarodon* and *Ophurus* this projection is missing and the dentary and surangular are not overlapped on the lateral surface. In *Conolophus* and *Cychura* the projection overlaps the dentary and surangular ventrally and projects very little anteriorly on the lateral surface of the dentary. *Amblyrhynchus* has a similar condition, however, there is a small anterior projection extending forward over part of the dentary. In *Brachylophus*, *Ctenosaura*, *Iguana* and *Sauromalus* the anterolateral projection overlapping the dentary and surangular is extended forward as an elongated triangular or rectangular process. The smallest angles of triangulation occur in *Ctenosaura* and *Brachylophus* in which the projection is elongated and splintlike. In *Iguana* and *Sauromalus* the anterior apex of the projection is rounded. The conditions of *Dipsosaurus* is similar to that of *Amblyrhynchus* and *Conolophus* where the lateral projection of the coronoid bone is mostly ventral in nature. There is, however, in *Dipsosaurus*, a small rounded anterior projection on the anterior border of the process.

TABLE 33
CORONOID BONES

Genus	Length			Width			Width-Length Ratio		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
<i>Amblyrhynchus</i>	6.4	9.7	12.0	6.9	9.3	11.4	900	935	968
<i>Brachylophus</i>	6.4	6.7	7.0	5.0	5.8	6.5	746	857	969
<i>Chalarodon</i>	1.4	1.6	1.9	1.5	1.6	1.8	933	941	947
<i>Conolophus</i>	15.1	21.8	25.0	9.0	12.4	14.3	521	571	596
<i>Ctenosaura</i>	4.3	6.6	9.5	3.0	4.8	7.4	684	717	778
<i>Cychura</i>	5.8	9.7	13.6	7.3	10.7	14.4	794	883	943
<i>Dipsosaurus</i>	3.2	3.6	4.3	4.2	4.4	4.9	761	798	873
<i>Iguana</i>	5.3	7.5	9.0	7.0	9.0	10.7	662	733	794
<i>Ophurus</i>	2.3	3.0	4.1	2.1	2.8	3.8	916	922	926
<i>Sauromalus</i>	3.0	5.2	8.1	2.7	4.5	6.9	771	875	936

Teeth

Teeth are pleurodont and are borne by the dentary in the lower jaw, the maxilla and premaxilla of the upper jaw, and the pterygoid of the palate. The possession of teeth and the numbers in each genus are summarized in table 34.

Pterygoid teeth are found in many genera on the pterygoid bones and their numbers are variable among individuals. Of five skulls of *Amblyrhynchus*

examined, only two had pterygoid teeth and these varied between 3-7 per side. These teeth were very tiny or represented only by a few sockets. In four skulls of *Brachylophus*, pterygoid teeth ranged in number from 1-8 per side. *Chalarodon* had well developed teeth in all four skulls examined, but with few in number, ranging from 2-4 per side. In five skulls of *Conolophus* only one had remnants of teeth. These remnants consisted of a few sockets on each pterygoid bone. In *Ctenosaura* all skulls had numerous well developed teeth numbering from 3-14 per side. A similar situation existed in *Cychura* with 1-10 teeth per side, *Iguana* with 8-27 teeth per side, and *Ophurus* with 4-9 teeth per side. In *Sauromalus* six skulls were examined and four had between 1-7 teeth per side. Teeth were absent in the other two skulls. Only in *Dipsosaurus* were there no pterygoid teeth or their vestiges in the four skulls examined. Camp (1923:367) omits *Dipsosaurus* from his list of Iguanidae lacking pterygoid teeth. This may be a mistake on his part or perhaps an examination of a larger series of skulls may reveal that some pterygoid teeth are present in some individuals of this genus.

Montanucci (1968:307-314) comments on the pterygoid teeth of *Iguana* and *Ctenosaura* and indicates that in *Iguana* the teeth have taken over the function of gripping as the lateral teeth are specialized for shearing. In *Ctenosaura* the pterygoid teeth share the gripping function with less specialized lateral teeth. He also indicates that there is a relationship between size of the skull and number of pterygoid teeth.

Premaxillary teeth are found in all ten genera. These are less cuspid than the lateral teeth in *Sauromalus* (Avery and Tanner, 1964:7-8). Observations on other genera indicates this is also the case for *Ctenosaura*, *Cychura*, *Iguana*, *Dipsosaurus* and *Ophurus*. In the other genera the premaxillary teeth bear secondary cusps.

Maxillary teeth are present in all genera and number from 15 to 26 per side in skulls examined. From our observations and those of Montanucci (1968:307-315) there appears to be a size-number relationship in iguanids, with smaller skulls always having less teeth than larger skulls in the same genus.

The cusps of the teeth differ considerably between genera. According to the system of Hotton (1955:91) the cusped character of the teeth of all genera would fit the category "high degree." The cusp number and shape varies within this category. *Chalarodon*, *Iguana* and *Ophurus* have small cusps and are poorly defined. *Brachylophus*, *Ctenosaura*, *Cychura*, *Dipsosaurus* and *Sauromalus* have cusps well defined but not separated by deep indentions. In *Amblyrhynchus* and *Conolophus* the lateral cusps are well defined and widely separated from the central cusp of the tooth. The number of cusps per tooth also varies from genus to genus. *Amblyrhynchus*, *Brachylophus*, *Chalarodon*,

and *Ophurus* are all tricusate. *Conolophus*, *Ctenosaura* and *Dipsosaurus* are tricusate with a few teeth bearing up to five cusps. In *Cyclura* and *Sauromalus* teeth with up to seven cusps are common and in *Sauromalus*, as many as nine occur. The most highly cusate teeth belong to *Iguana* which exhibits up to 13 cusps per tooth in some individuals. Hotton (1955) and Montanucci (1968) attribute the number of cusps per tooth to the kind of diet and specialized functions (gripping, shearing, masticating) of the teeth. It appears that lizards with similar diet and eating habits have similar dentition.

Dentary teeth are found in all ten genera. The number of teeth per bone is slightly larger than that for the maxilla of the same lizard. This is because the upper teeth are found on the premaxilla as well. The sum of one half of the teeth of the premaxillae and all the maxillary teeth of one side should roughly equal the number of dentary teeth.

In general, teeth of the dentary are similar to those of the maxilla and premaxilla and the size-number relationship exists for them as well.

TABLE 34
TEETH

Genus	Pterygoid per side	Premaxilla	Maxillary per side	Dentary per side
<i>Amblyrhynchus</i>	0-7	7	17-21	17-24
<i>Brachylophus</i>	1-8	6-7	16-19	18-21
<i>Chalarodon</i>	2-4	6	16-18	19-21
<i>Conolophus</i>	None	7-8	15-20	17-21
<i>Ctenosaura</i>	3-14	7-8	20-26	20-33
<i>Cyclura</i>	0-10	6-10	19-23	22-28
<i>Dipsosaurus</i>	None	7-8	16-19	20-23
<i>Iguana</i>	8-52	6-7	20-26	19-30
<i>Ophurus</i>	4-9	6	15-19	16-23
<i>Sauromalus</i>	0-7	5-6	16-20	15-25

Hyoid Elements

The hyoids of the iguanines (fig. 8) are basically alike in structure. The hyoid is always cartilagenous in nature and consists of a central disc, the basihyal, to which is attached an anterior projection, the glossohyal or processes entoglossus; an anterolateral projection on each side, the hypohyal; and two ceratobranchials, projecting posteriorly on each side. The medial ceratobranchials (II) are paired and extend posteriorly. In *Iguana* these are involved in operating the dewlap. The lateral ceratobranchials (I) project posterolaterally from the basihyal and articulate with the hypohyal by means of a lateral ceratohyal which extends between the lateral terminations of each cartilage.

Unfortunately hyoids are seldom preserved in museum collections. As a result only one or two hyoids from each genus were examined, but some differ-

ences between genera can be noted. The shape of the hyoid corresponds to the shape of the animal. Iguanines that are dorsoventrally flattened normally have short hyoids with a large lateral spread of the ceratohyals and ceratobranchial I's. Such is found in *Conolophus*, *Cyclura*, and *Sauromalus*. Most of the remaining genera are compressed laterally, and the spread of lateral elements of the hyoid in these is less than in the dorsoventrally flattened forms.

The basihyal is broader than long in some dorsoventrally flattened forms such as *Sauromalus* but is elongated in *Conolophus*, *Ctenosaura*, *Cyclura*, and the other genera. *Sauromalus* also differs from the other genera in that the ceratobranchial II's are spread apart in life.

Individual elements of the hyoid show some differences which may be of phylogenetic importance. The dorsomedial portion of the ceratohyal is enlarged into a triangular to spoon shaped flange in *Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, and *Sauromalus*. In *Ophurus* this flange is extremely small and is absent in *Chalarodon*. All other elements of the hyoid differ in length but not in shape.

Sternum and Ribs

The sterna and ribs of the iguanines have been discussed by Etheridge (1965) who examined the relationships of the abdominal skeleton of iguanids to the sternum and figured those of *Amblyrhynchus* and *Chalarodon*. Etheridge indicates that abdominal or inscriptional ribs are associated with the sternum in at least four different ways in the family Iguanidae. Three of Etheridge's four patterns include iguanines. In one type "all of the inscriptional ribs posterior to the xiphisternum are attached to their corresponding dorsal ribs and end free without reaching the ventral midline" (Etheridge, 1965:163). Included in this group are *Sauromalus* and some individuals of *Conolophus*, *Amblyrhynchus*, *Cyclura*, and *Ctenosaura*. A second type according to Etheridge (1965:163) "is similar to the preceding except that one or two of the inscriptional rib pairs, either the first or second, or both may join one another at the ventral midline to form continuous chevrons." *Iguana*, *Brachylophus* and some *Conolophus*, *Amblyrhynchus*, *Cyclura* and *Ctenosaura* have this type of attachment. A third pattern involves *Chalarodon* and *Ophurus* and according to Etheridge (1965:166) "consists entirely of paired elements that are free of attachment either to their corresponding dorsal ribs or to one another at the ventral midline. Members of the pair may approach one another very closely, touch, or even overlap mid-ventrally, but never join one another to form a continuous chevron". It is perplexing to note that although Etheridge mentions having examined *Dipsosaurus*, he fails to assign it an abdominal skeletal type.

- A. *Amblyrhynchus cristatus*. BYU 22810. $\times 1.25$
 B. *Brachylophus fasciatus*. MCZ 15009. $\times 2.0$
 C. *Chalarodon madagascariensis*. MCZ 11531. $\times 4.0$
 D. *Conolophus pallidus*. MCZ 79772. $\times 1.0$
 E. *Ctenosaura pectinata*. MCZ 2176. $\times 1.5$

Key to symbols used in Figure 1.

ec-ectopterygoid
 fe-fenestra exonarina
 fr-frontal
 ju-jugal
 mx-maxilla
 na-nasal
 ob-orbit
 pal-palatine
 par-parietal
 pf-pineal foramen
 pm-premaxilla
 pot-postorbital
 prf-prefrontal
 pt-ptyergoid
 ptf-postfrontal
 qu-quadrate
 stf-supratemporal fossa
 so-supraoccipital
 sq-squamosal

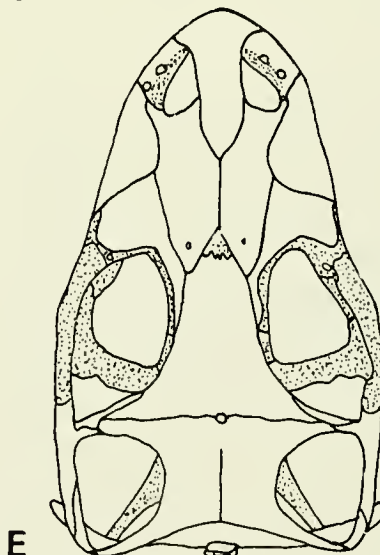
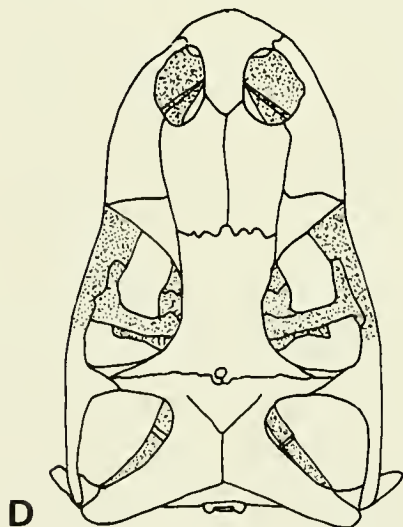
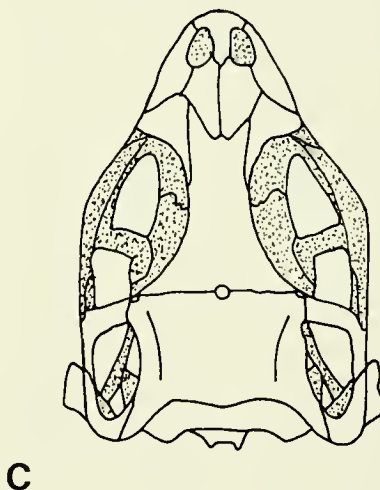
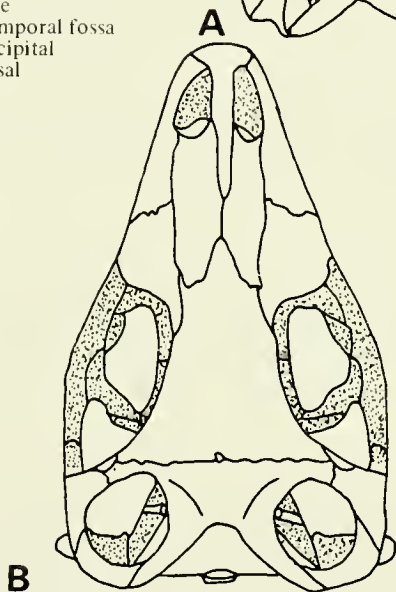
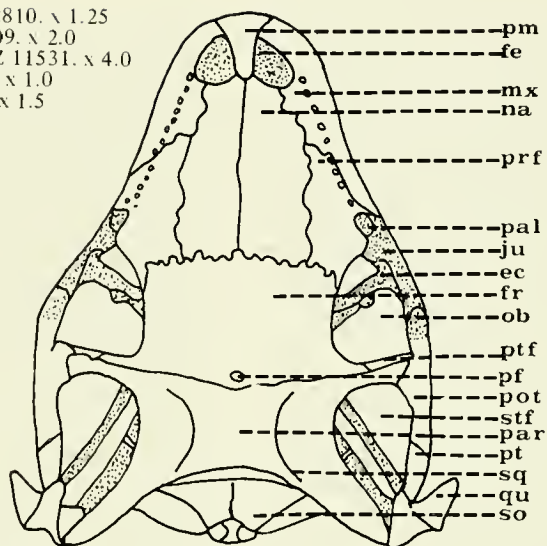


Figure 1. Dorsal view of skull.

- A. *Cyclura macleayi*. MCZ 6915. x 0.75
B. *Dipsosaurus dorsalis*. BYU 21726. x 2.0
C. *Iguana iguana*. BYU 22795. x 1.0
D. *Oplurus sebae*. MCZ 37191. x 3.0
E. *Sauromalus obesus*. BYU 21728. x 2.0

Key to symbols used in Figure 2.

- ec-ectopterygoid
- fe-fenestra exonarina
- fr-frontal
- ju-jugal
- mx-maxilla
- na-nasal
- ob-orbit
- pal-palatine
- par-parietal
- pf-pineal foramen
- pm-premaxilla
- pot-postorbital
- prf-prefrontal
- pt-pterygoid
- ptf-postfrontal
- qu-quadrate
- stf-supratemporal fossa
- so-supraoccipital
- sq-squamosal

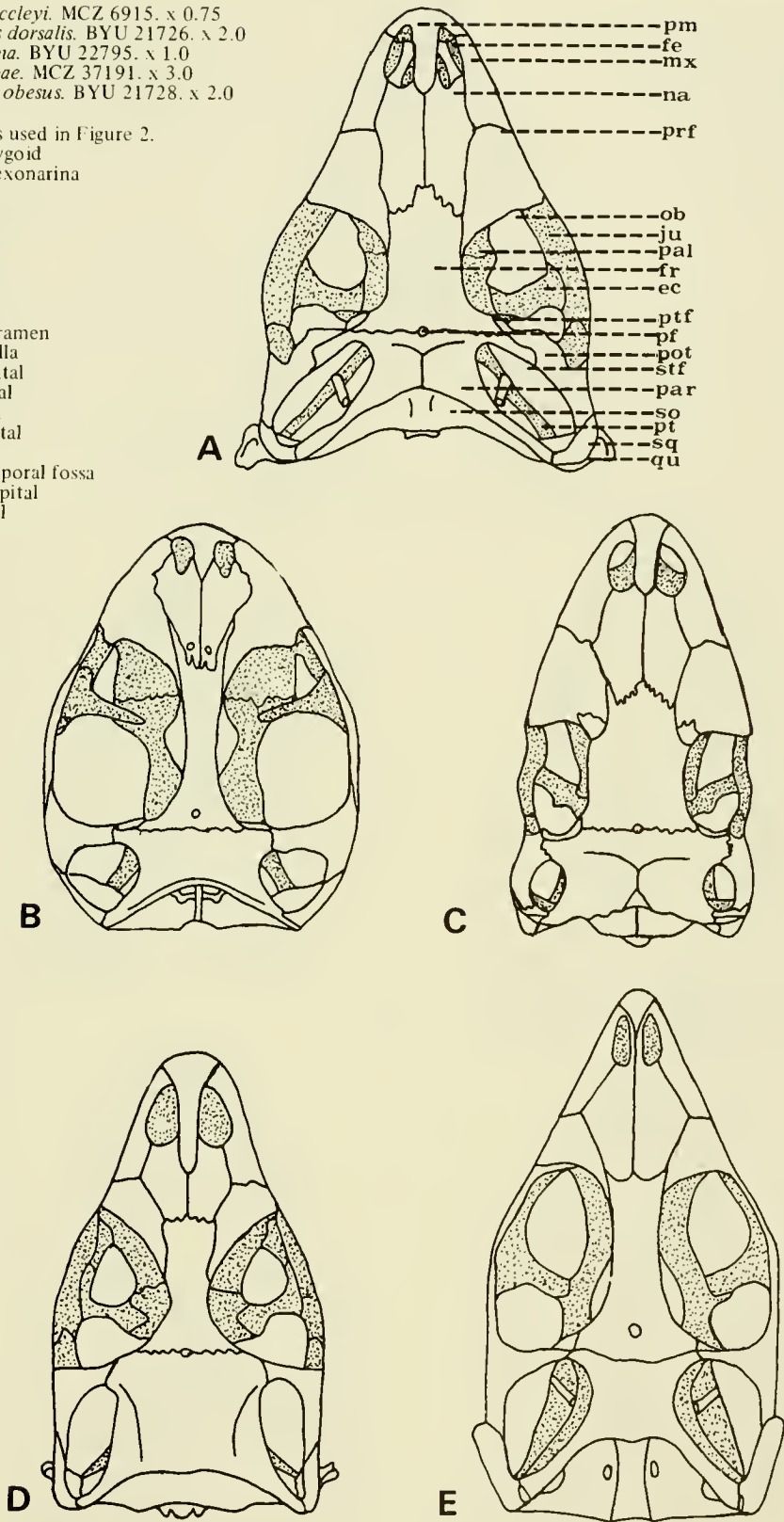


Figure 2. Dorsal view of skull.

- A. *Amblyrhynchus cristatus*. BYU 22810. $\times 1.25$
 B. *Brachylophus fasciatus*. MCZ 15009. $\times 2.0$
 C. *Chalarodon madagascariensis*. MCZ 11513. $\times 4.0$
 D. *Conolophus pallidus*. MCZ 79772. $\times 1.0$
 E. *Ctenosaura pectinata*. MCZ 2176. $\times 1.5$

Key to symbols used in Figure 3.

- bo-basioccipital
 bp-basipterygoid process
 bs-basisphenoid
 ec-ectopterygoid
 ju-jugal
 mx-maxilla
 pal-palatine
 pm-premaxilla
 po-postorbital
 pp-parasphenoid process
 pr-pyriform recess
 pt-ptyergoid
 ptt-ptyergoid teeth
 qu-quadrates
 sq-squamosal
 vo-vomer

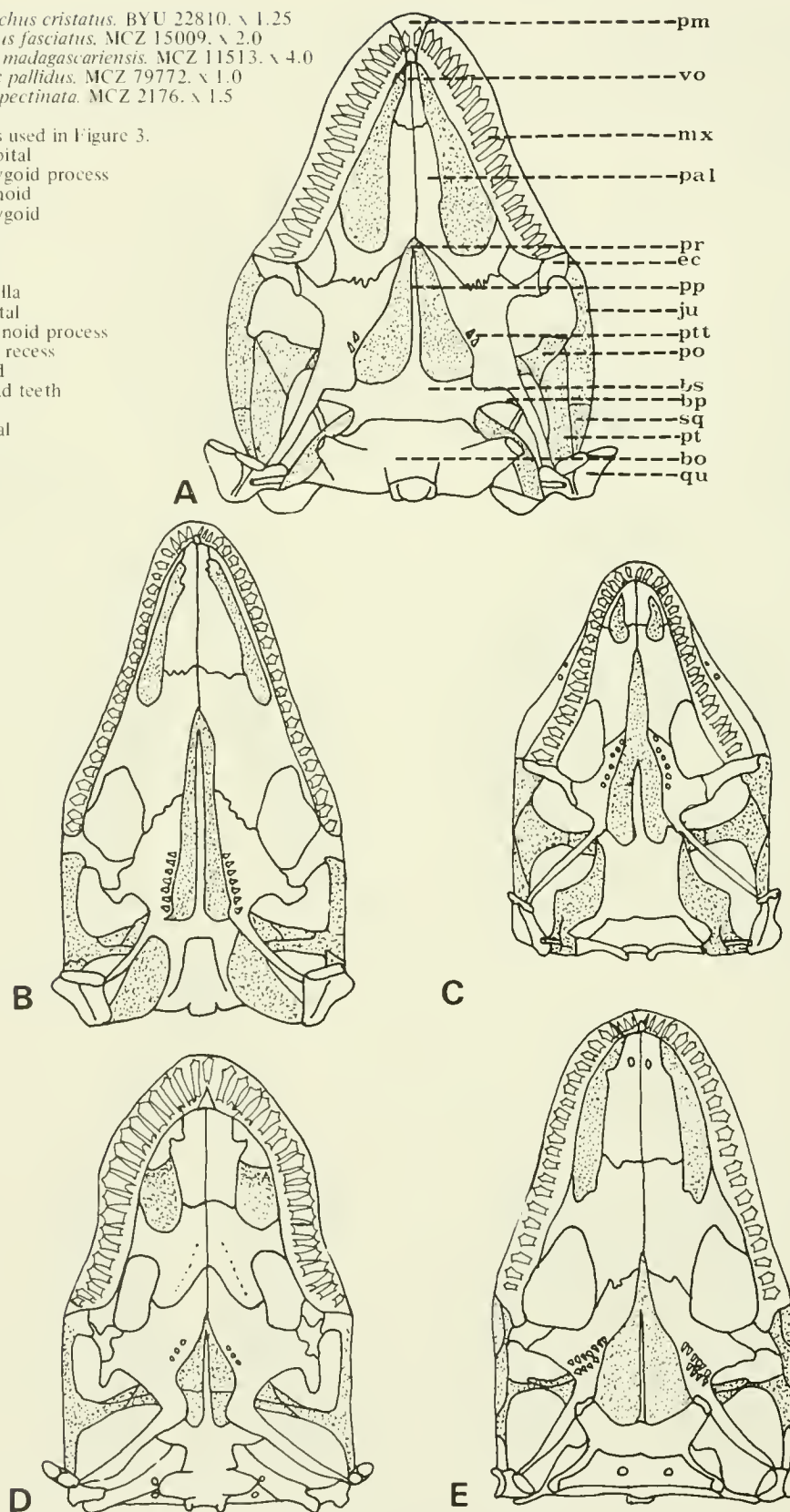


Figure 3. Ventral view of skull.

- A. *Cyclura maccleyi*. MCZ 6915. $\times 0.75$
B. *Dipsosaurus dorsalis*. BYU 21726. $\times 2.0$
C. *Iguana iguana*. BYU 22795. $\times 1.0$
D. *Oplurus sebae*. MCZ 37191. $\times 3.0$
E. *Sauromalus obesus*. BYU 21728. $\times 2.0$

Key to symbols used in Figure 4.

- bo-basioccipital
bp-basipterygoid process
bs-basisphenoid
ec-ectopterygoid
ju-jugal
mx-maxilla
pal-palatine
pm-premaxilla
po-postorbital
pp-parasphenoid process
pr-pyriform process
pt-ptyergoid
ptt-pterygoid teeth
qu-quadrate
sq-squamosal
vo-vomer

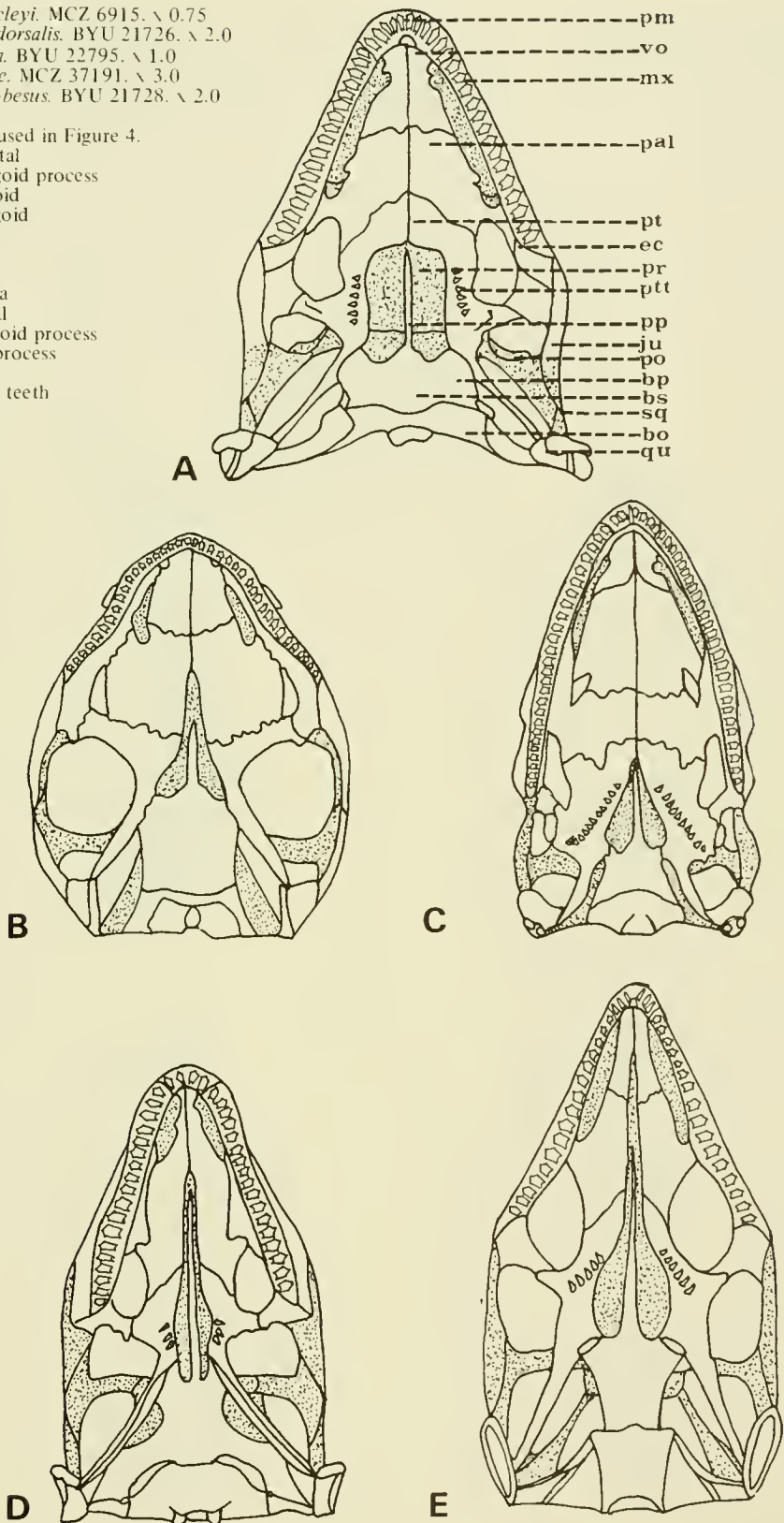


Figure 4. Ventral view of skull.

- A. *Amblyrhynchus cristatus*. BYU 22810. $\times 1.25$
 B. *Brachylophus fasciatus*. MCZ 15009. $\times 2.0$
 C. *Chalarodon madagascariensis*. MCZ 11531. $\times 4.0$
 D. *Conolophus pallidus*. MCZ 79772. $\times 1.0$
 E. *Ctenosaura pectinata*. MCZ 2176. $\times 1.5$

Key to symbols used in Figure 5.

- an-angular
 ar-articular
 co-coronoid
 de-dentary
 ec-ectopterygoid
 ep-epiterygoid
 fe-fenestra exonarina
 fr-frontal
 ju-jugal
 la-lacrima
 mx-maxilla
 na-nasal
 ob-orbit
 pm-premaxilla
 po-postorbital
 pp-parasphenoid process
 prf-prefrontal
 pr-parietal
 pt-ptyergoid
 ptf-postfrontal
 qu-quadrate
 sq-squamosal
 sr-surangular

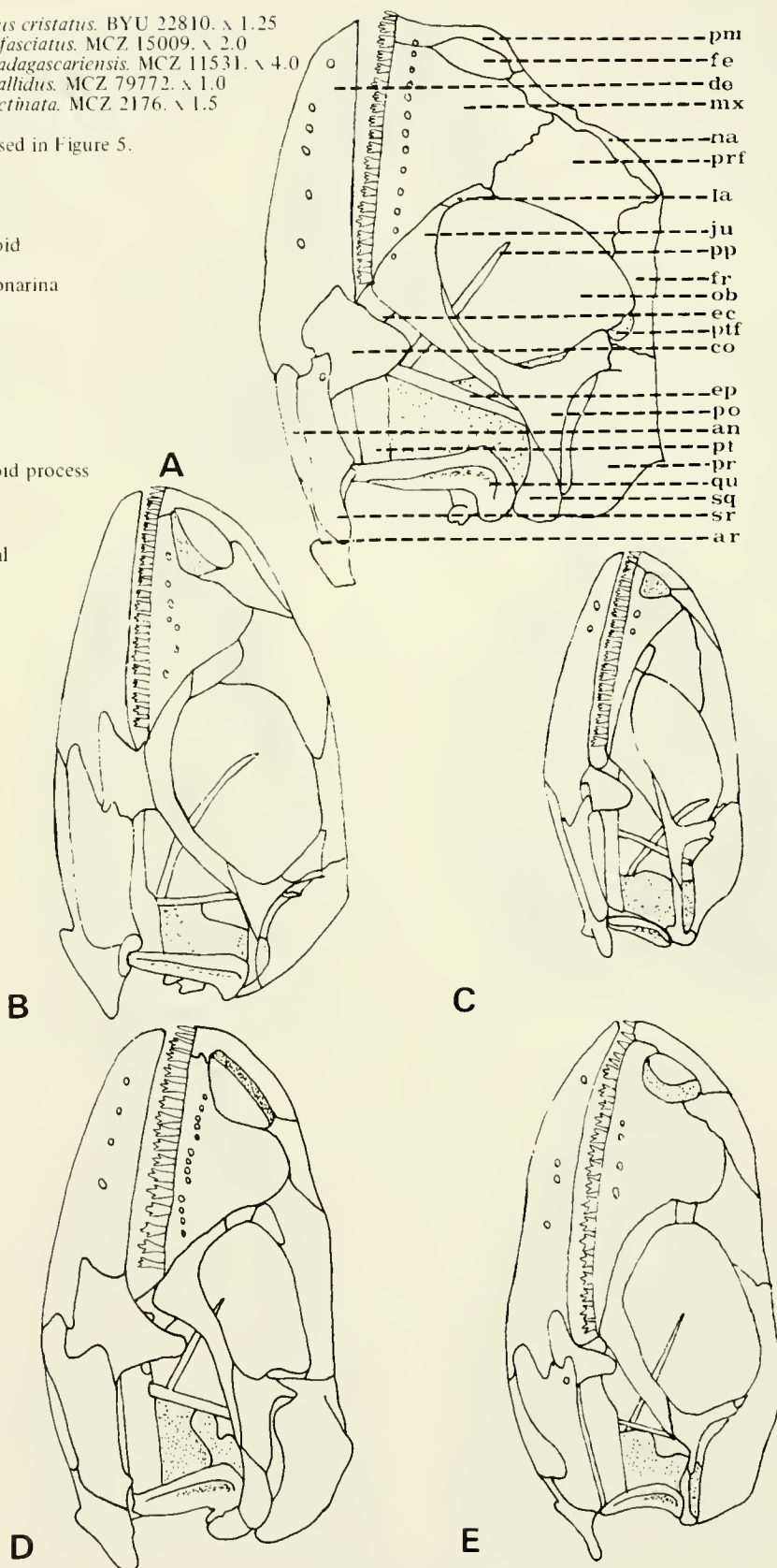


Figure 5. Lateral view of skull.

- A. *Cyclura macclayi*. MCZ 6915. x 0.75
- B. *Dipsosaurus dorsalis*. BYU 21726. x 2.0
- C. *Iguana iguana*. BYU 22795. x 1.0
- D. *Oplurus sebae*. MCZ 27191. x 3.0
- E. *Sauromalus obesus*. BYU 21728. x 2.0

Key to symbols used in Figure 6.

- ar-articular
- co-coronoid
- de-dentary
- ec-ectopterygoid
- ep-epipterygoid
- fe-fenestra exonarina
- ju-jugal
- la-lacrima
- mx-maxilla
- na-nasal
- ob-orbit
- pm-premaxilla
- po-postorbital
- pp-parasphenoid process
- prf-prefrontal
- pr-parietal
- pt-ptyergoid
- ptf-postfrontal
- qu-quadrata
- sq-squamosal
- sr-surangular

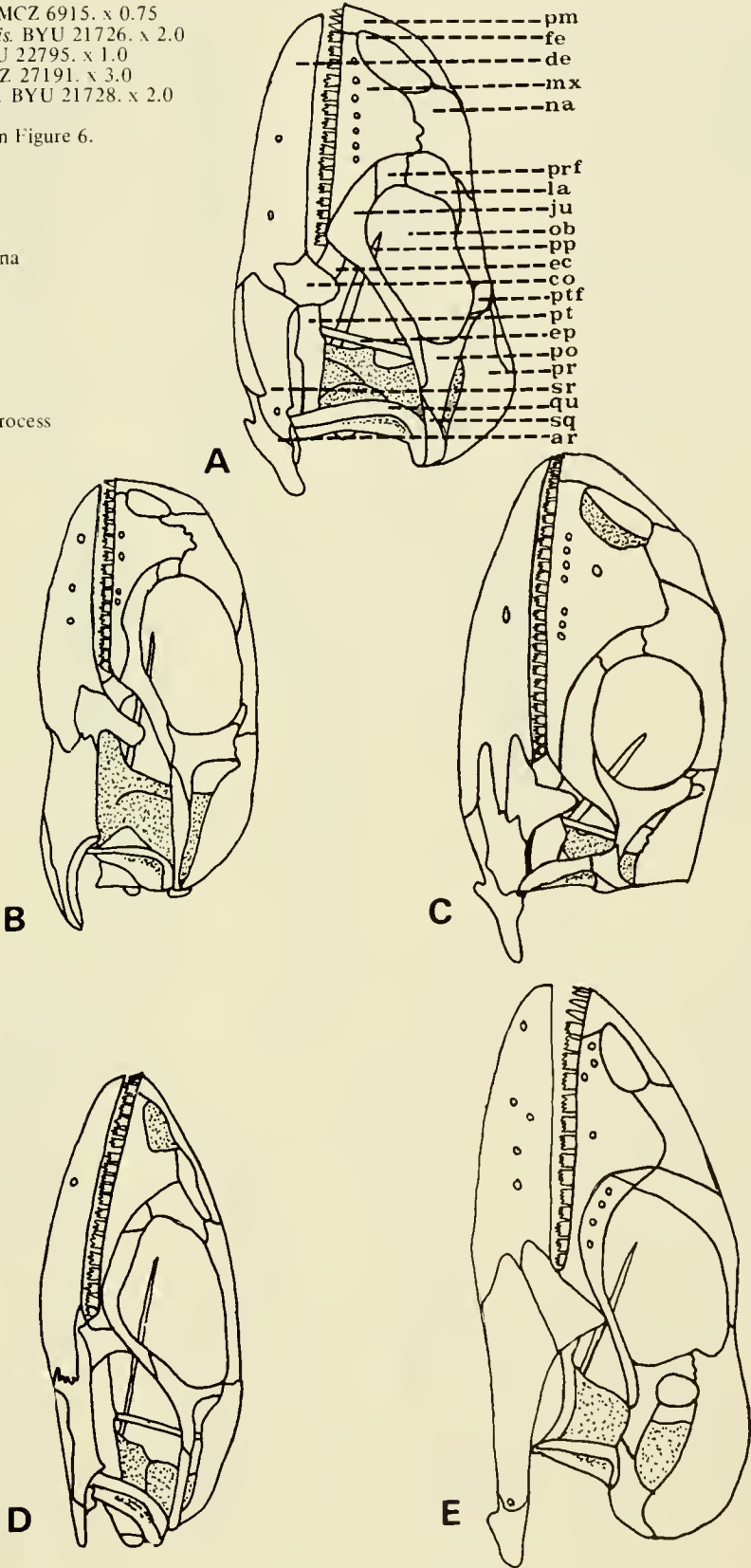


Figure 6. Lateral view of skull.

- A. *Amblyrhynchus cristatus*. BYU 22810. $\times 1.75$
 B. *Brachylophus fasciatus*. MCZ 15009. $\times 2.0$
 C. *Chalarodon madagascariensis*. MCZ 11531. $\times 4.0$
 D. *Conolophus pallidus*. MCZ 79772. $\times 1.0$
 E. *Ctenosaura pectinata*. MCZ 2176. $\times 1.5$
 F. *Cyclura macclayi*. MCZ 6915. $\times 10.75$
 G. *Dipsosaurus dorsalis*. BYU 21726. $\times 2.0$
 H. *Iguana iguana*. BYU 22795. $\times 1.0$
 I. *Oplurus sebae*. MCZ 37191. $\times 3.0$
 J. *Sauromalus obesus*. BYU 21728. $\times 2.0$

Key to symbols used in Figure 7.

- aif- anterior inferior alveolar foramen
 an- angular
 anp- angular condyle
 co- coronoid
 de- dentary
 sp- splenial
 sr- surangular

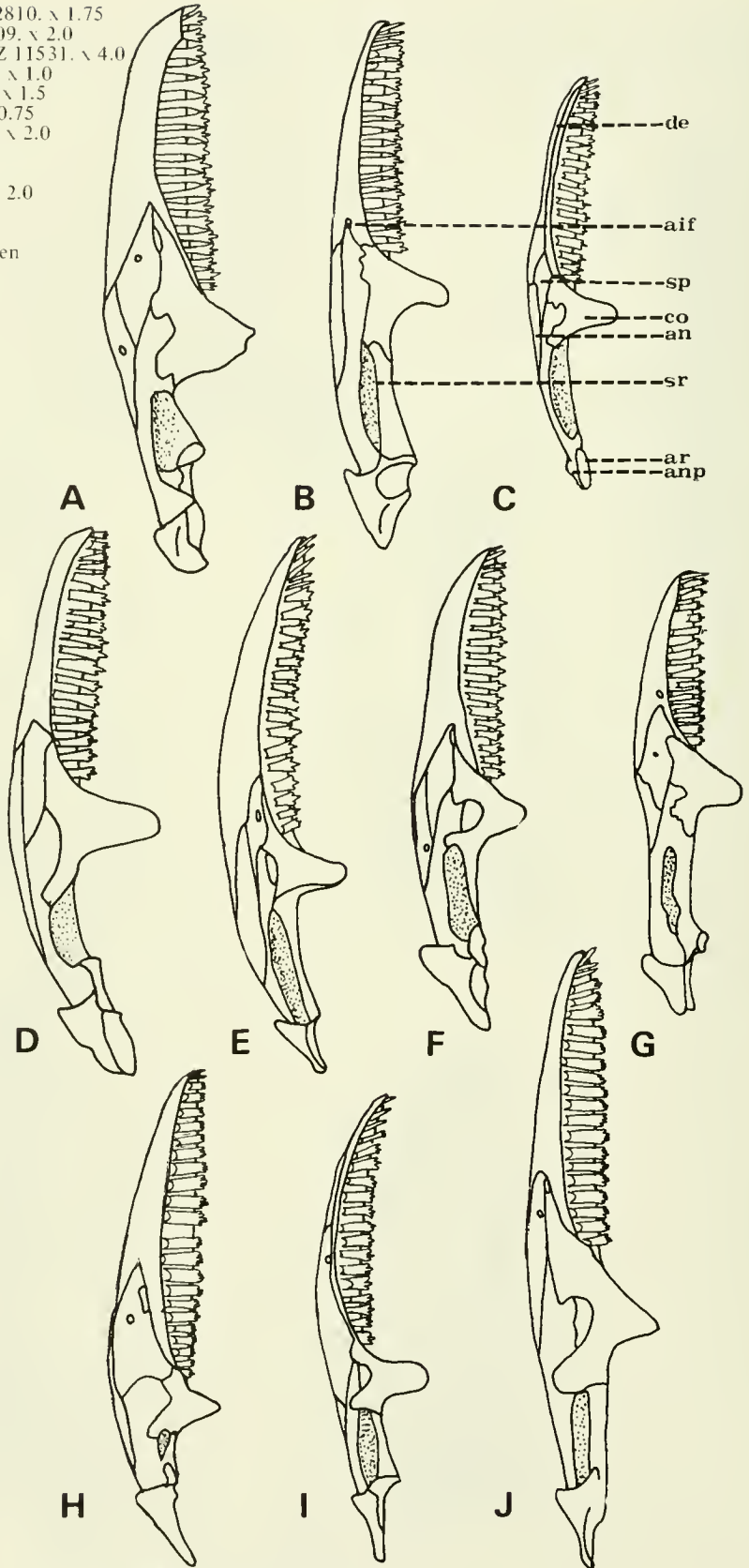


Figure 7. Medial view of mandible.

- A. *Amblyrhynchus cristatus*. BYU 22810. $\times 10.75$
B. *Brachylophus fasciatus*. BYU 23743. $\times 1.0$
C. *Chalarodon madagascariensis*. MCZ 11522. $\times 4.0$
D. *Conolophus suberistatus*. MCZ 2027. $\times 0.75$
E. *Ctenosaura pectinata*. BYU 22796. $\times 10.75$
F. *Cyclura carinata*. MCZ 59255. $\times 1.0$
G. *Dipsosaurus dorsalis*. BYU 21726. $\times 1.5$
H. *Iguana iguana*. BYU 22852. $\times 1.0$
I. *Ophurus sebae*. MCZ 27188. $\times 3.0$
J. *Sauromalus obesus*. MCZ 8894. $\times 1.5$

Key to symbols used in Figure 8.
bh-basihyal
cb I-ceratobranchial I
cb II-ceratobranchial II
ch-ceratohyal
gh-glossohyal
hh-hypohyal

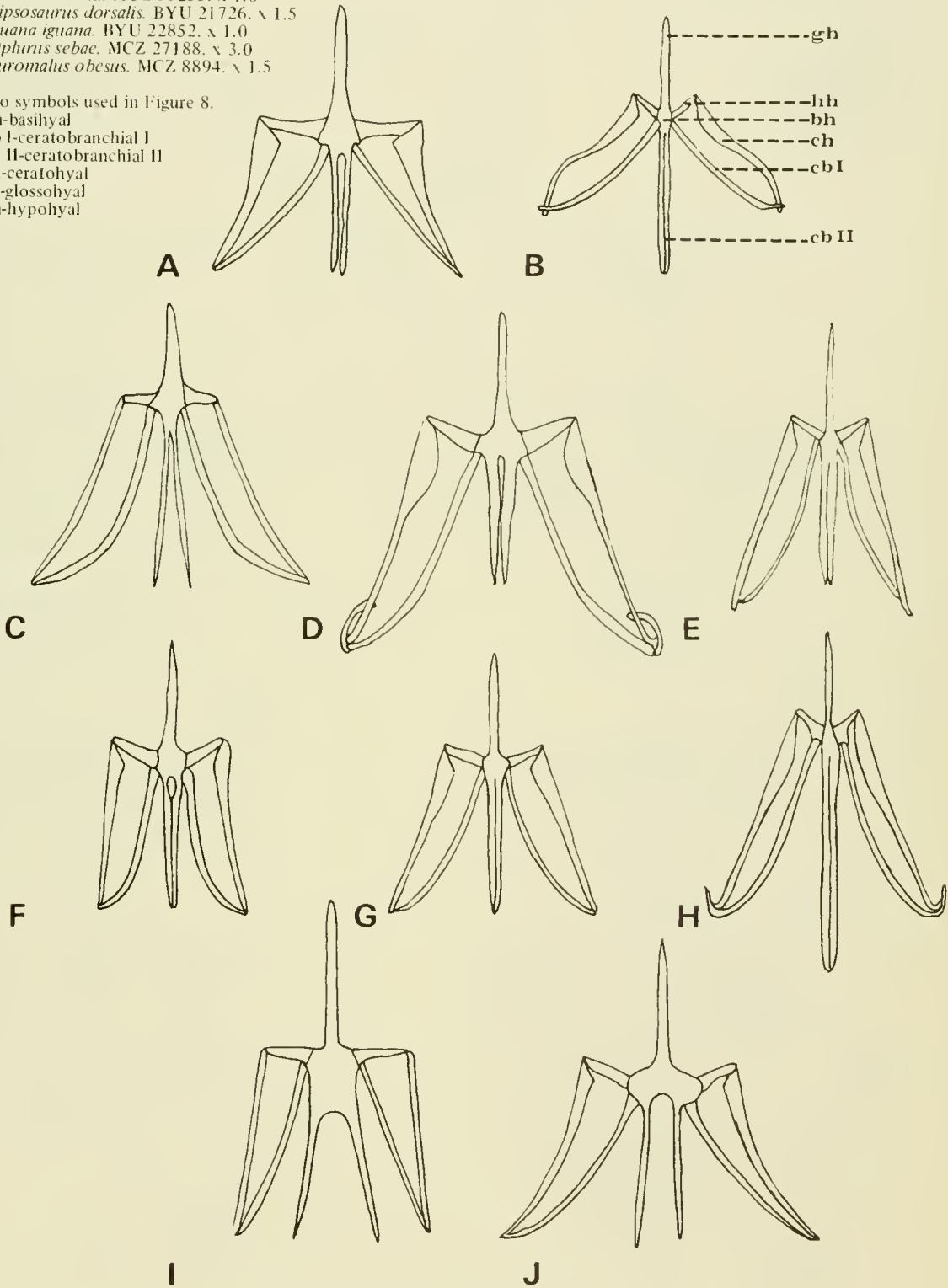


Figure 8. Ventral view of Hyoid Bones.

- A. *Amblyrhynchus cristatus*. MCZ 2006. $\times 1.0$
 B. *Brachylophus fasciatus*. MCZ 15008. $\times 2.0$
 C. *Chalarodon madagascariensis*. MCZ 11531. $\times 4.0$
 D. *Conolophus pallidus*. MCZ 79772. $\times 1.0$
 E. *Ctenosaura pectinata*. MCZ 2176. $\times 1.5$

Key to symbols used in Figure 9.

- cl-clavicle
 ic-interclavicle
 sc-sternal cartilage
 sf-sternal fontanelle
 sr-sternal ribs
 xr-xiphisternal ribs

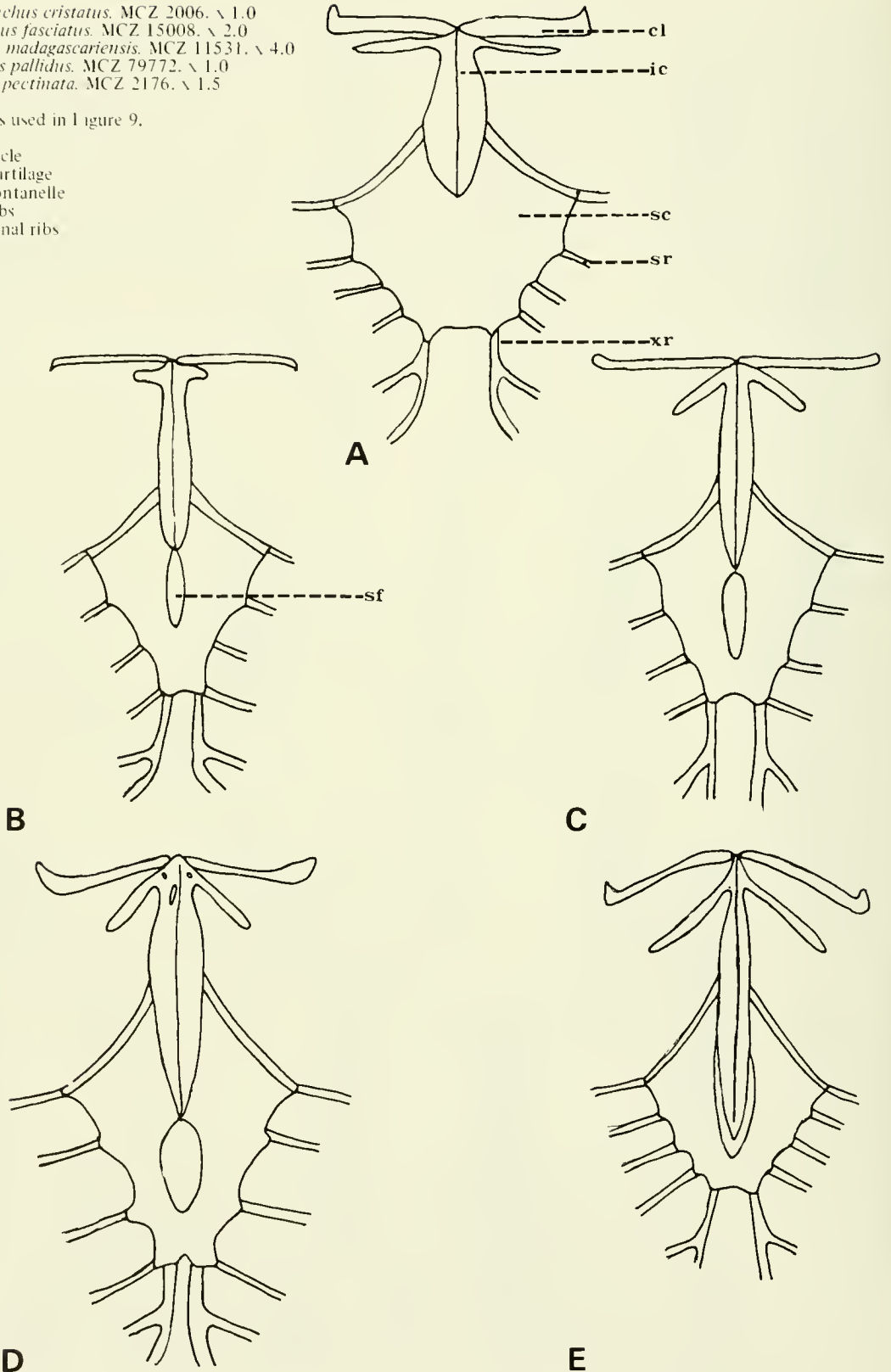


Figure 9. Ventral view of sternum.

- A. *Cyclura maccreyi*. MCZ 6915. $\times 1.0$
B. *Dipsosaurus dorsalis*. BYU 21726. $\times 2.0$
C. *Iguana iguana*. MCZ 54989. $\times 1.0$
D. *Oplurus sebae*. MCZ 37191. $\times 3.0$
E. *Sauromalus obesus*. MCZ 8894. $\times 2.0$

Key to symbols used in Figure 10.

- cl-clavicle
- ic-interclavicle
- sc-sternal cartilage
- sf-sternal fontanelle
- sr-sternal ribs
- xr-xiphisternal ribs

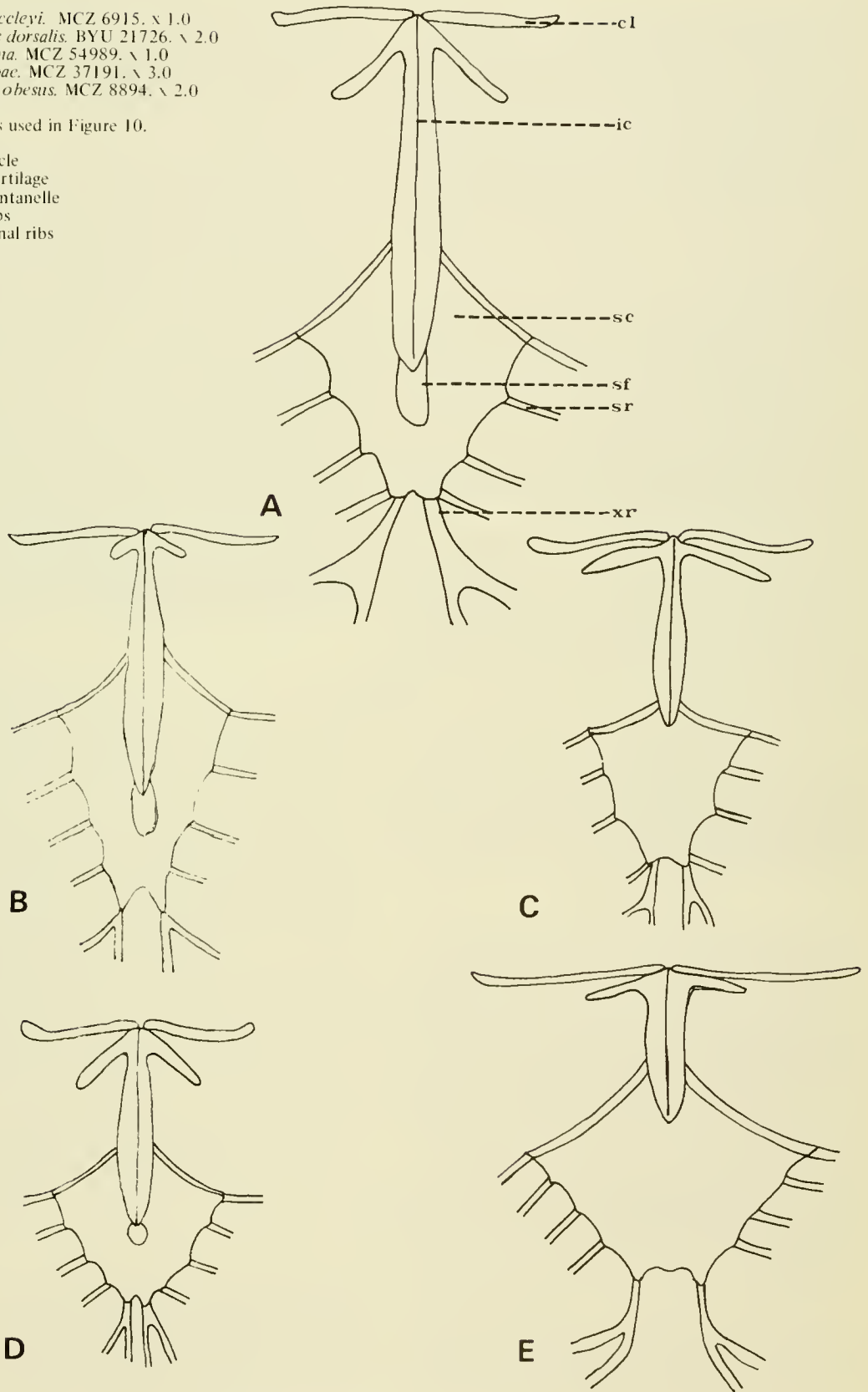


Figure 10. Ventral view of sternum.

The several specimens of *Dipsosaurus* examined conformed to Etheridge's second type.

The sternum of all iguanines examined (Figs. 9 and 10) consists of a sternal cartilage which articulates laterally with four pairs of sternal ribs and posteriorly with two pairs of xiphoid ribs. Anteriorly the sternal cartilage is attached to and partially surrounds a "T" shaped interclavicle. The arms of the "T" are of different lengths and leave the body of the interclavicle.

Sternal cartilage

Sternal cartilage corresponds in shape to general shape of the lizards. In dorsoventrally flattened forms the cartilage is wider than long. This situation exists in *Sauromalus* and *Amblyrhynchus* and is about equally as wide as long in *Ctenosaura* and *Cyclura*. All other genera have elongated sterna.

The sterna in some forms is pierced by sternal fontanelles. Camp (1923:409-410) reports fontanelles to be lacking in *Chalarodon* and *Sauromalus*. He found a single medial fontanelle in *Iguana* and *Dipsosaurus*. Two fontanelles were not recorded for any iguanines. We have found fontanelles to be lacking in *Amblyrhynchus*, *Chalarodon*, and *Sauromalus*. A single central fontanelle exists in *Brachylophus*,

Conolophus, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, and *Iguana*. These openings usually surround the terminal end of the body of the interclavicle. The one sternum of *Ophurus* examined has two small fontanelles along the center line.

Interclavicle

Interclavicle differs in size of the body, the angles of the anterior arms to the body, and the length of the arms. The arms attach to the body at 90° angles in *Amblyrhynchus*, *Brachylophus*, *Iguana*, and *Sauromalus*. The arms are attached at 45° angles in *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, and *Ophurus*. In *Dipsosaurus* the interclavicle arms are in an intermediate position between the two preceding groups. The arms are attached at approximately a 30° angle to the body.

The length of the interclavicle arms are short in *Brachylophus* and *Dipsosaurus* being about one quarter the length of the interclavicle body. The longest arms in relation to the body are those of *Amblyrhynchus*, *Sauromalus* and *Iguana*, being about equal to the length of the body. In *Ophurus*, *Ctenosaura*, *Chalarodon*, *Conolophus*, and *Cyclura* the arms are two-thirds the length of the body.

MYOLOGY

In order to avoid confusion, the terminology used for the following description of the muscles is that of Robison and Tanner (1962), Avery and Tanner (1964), and Jenkins and Tanner (1968). Any deviations will be noted in the text.

Throat Musculature

M. Intermandibularis anterior superficialis

M. Intermandibularis anterior superficialis (Figs. 11 and 12) is a short straplike muscle connecting the rami of the mandibles in the area between the origin of the genioglossus and the first mandibulohyoideus muscle. The body lies superficial to the intermandibularis anterior profundus, mandibulohyoideus II and the genioglossus muscle. It is overlain superficially by the skin.

It arises from the oral membrane, the anterior fibers of the intermandibularis anterior profundus, and the crista dentalis ligament. The muscle insertion is with fibers of its opposite equivalent along the midline raphe.

This muscle is constant in all genera examined with the following exceptions. It was found to be absent in one juvenile *Dipsosaurus* examined and narrow and reduced in adults. The muscle was also found reduced and narrow in *Iguana* where it contributes to the anterior margin of the muscular contents

of the dewlap. In the remaining genera the muscle is sheetlike with the width at least half the length.

M. Intermandibularis anterior profundus

M. Intermandibularis anterior profundus (Figs. 11 and 12) is a continuous sheet of muscle lying superficial to the majority of throat musculature and just deep to the skin. The muscle arises from the medial surface of the splenial and coronoid bones and from the crista dentalis by a tendon. The anterior fibers extend anteriomesially across the throat to insert on the ventral midline raphe. The posterior fibers also insert on the midline raphe after arising via several interdigitations with the first mandibulohyoideus muscle.

The muscle is relatively consistent in the iguanines examined. In *Iguana* the intermandibularis anterior profundus extends deep into the dewlap with the fibers ending about one-third the distance from the ventral border. It also forms the bulk of the muscular contents of the dewlap.

M. Intermandibularis posterior

M. Intermandibularis posterior (Figs. 11, 12, 24 and 25) is a thin sheet overlying the angle of the jaw and covering superficially, the posterior fibers of the intermandibularis anterior profundus. The muscle sheet is extremely thin in the posterior extremities

and thickens towards its anterior extremes. The posterior origin of this muscle is from the lateral surface of the mandible beginning at the midpoint of the retroarticular process. Anteriorly the muscle originates as the last two or three interdigitations of the anterior profundus muscle with which it is continuous. Its insertion on the midline raphe is characterized by a wide aponeurosis which leaves both sets of fibers from each side separated in some specimens.

Posteriorly the intermandibularis posterior is continuous with the constrictor colli from which it can be delimited by a natural separation of the muscle fiber bundles. The possession of this separation is variable in the genera examined. In *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Dipsosaurus*, *Iguana*, and *Ophurus* the constrictor colli and intermandibularis posterior are closely associated along their entire common border. In *Conolophus* and *Ctenosaura* the two muscles are separated laterally at the angle of the jaw with part of the pterygomandibularis being visible between them. In *Cychura* and *Sauromalus* the edges of the two muscles become more separated towards the midline raphe. In *Iguana* the intermandibularis posterior extends deep into the dewlap ending about a third of the way to the ventral border. It also forms the posterior portion of the dewlap's muscular content.

M. Mandibulohyoideus I

M. Mandibulohyoideus I (Figs. 11 and 12) is a long triangular muscle which extends two-thirds of the length of the mandible, and lies lateral to the second mandibulohyoideus, mesial to the mandibular rami, and anterior to the insertion of the sternohyoideus. This muscle lies dorsal to the intermandibularis muscle and ventral to the genioglossus, hyoglossus, mandibulohyoideus III, and the pterygomandibularis muscles. At its anterior end, the mandibulohyoideus I interdigitates at right angles with the fibers of the intermandibularis anterior profundus.

The mandibulohyoideus I originates along the ventromesial surface of the dentary and a small part of the angular, from the posterior border of the intermandibularis anterior superficialis, posteriorly to the mass of the pterygomandibularis. It inserts just posterolateral to the insertion of the mandibulohyoideus II along the anterolateral border of the distal three-fourths of the first ceratobranchial.

There is no deviation from this pattern in the general examined.

M. Mandibulohyoideus II

M. Mandibulohyoideus II (Figs. 11 and 12) is a small elongated muscle tapering at both ends, lying mesial to the mandibulohyoideus I and inserting alongside its opposite equivalent on the midventral raphe. It lies deep to the intermandibularis muscle and superficial to the tongue, the genioglossus, and

the hyoglossus.

The origin of the mandibulohyoideus muscle is a narrow tendon, an anterior extension of the midline raphe, from the capsule of cartilage overlying the mandibular symphysis. The muscle inserts on the anterior border of the proximal end of the first ceratobranchial, anteromesial to the insertion of the first mandibulohyoideus. A similar situation exists in all the genera examined.

M. Mandibulohyoideus III

M. Mandibulohyoideus III (Figs. 13 and 14) is a thick straplike muscle extending over the pterygomandibularis and with attachments to it by connective tissue. The course of this muscle is nearly parallel to the mandibular ramus on each side. It lies between the ceratohyal and the pterygomandibularis.

In all genera this muscle arises from the ventromesial surface of the dentary and angular bones between the anterior and posterior myohyoid foramina. The narrow insertion of this muscle is on the lateral surface of the ceratohyal, distal to its midpoint.

M. Genioglossus

M. Genioglossus (Figs. 11, 12, 13 and 14) is a thick bandlike muscle in all genera which, with its partner on the opposite side, occupies a large area between the mandibular rami. Its position is ventral to the tongue and anterior to the basihyal. The first, second, and third mandibulohyoideus muscles and the intermandibularis muscle all lie ventral to it.

The genioglossus originates along the ventral and mesial surfaces of the anterior one-sixth of the mandibular ramus, and dorsal to Meckel's canal. The mesial fibers extend posteriorly, while the lateral fibers turn dorsally and laterally before passing posteriorly.

M. Hyoglossus

M. Hyoglossus (Figs. 13 and 14) is a thick broad muscle lying lateral to the basihyal and the second ceratobranchial and basial to the mandible, the mandibulohyoideus III and the pterygomandibularis. The mandibulohyoideus I and II muscles and the anterior portion of the mandibulohyoideus III lies superficial to it. The hyoglossus muscle lies ventral to the ceratohyal and the oral membranes.

The origin of this muscle is along the anterolateral face of the distal two-thirds of the first ceratobranchial and dorsal to the insertion of the mandibulohyoideus I muscle. The muscle traverses an anterior path to interdigitate with the genioglossus near the proximal end of the hypohyal and to form the main body of the tongue.

M. Branchiohyoideus

M. Branchiohyoideus (Figs. 13 and 14) lies dorsal to the hyoglossus, between the ceratohyal and the

first ceratobranchial of the hyoid bone. This muscle lies just ventral to the oral membrane which in turn lies ventral to the massive pterygomandibularis muscle.

The branchiohyoideus has its origin from the posteromesial surface of the posterior two-thirds of the ceratohyal. Its path passes parallel to the two hyoid limbs, and inserts near the distal end of the first ceratobranchial.

In *Sauromalus* the insertion on the first ceratobranchial is narrow whereas the insertion in the other genera covers over half the distal portion of the first ceratobranchial.

M. Sternohyoideus

M. Sternohyoideus (Figs. 11, 12, 13, 14, 25 and 26) is an extensive muscle sheet, occupying a large area posterior to the first ceratobranchial cartilage and anterior to the sternum and clavicle. Its position is deep to the intermandibularis and the constrictor colli anteriorly, and to the episternocleidomastoideus, the trapezius, a small part of the levator scapulae profundus, pharyngeal membranes, trachea, clavicle, and the clavodeltoideus.

There has been considerable confusion in the literature concerning the limits of this muscle. Davis (1934:19) considers the superficial layer to be divisible into three parts in *Crotaphytus*. One of these muscles he calls the omohyoideus. Robison and Tanner (1962:6) consider this muscle continuous in the same genus. Oelrich (1956:51-52) treats this muscle in *Ctenosaura* as being continuous but owing to the different origin and direction of the fibers, he separates the layers into omohyoideus and sternohyoideus. Kesteven's studies (1944:245-246) on the agamid, *Physignathus*, suggests a separation in young specimens and treats these layers as consisting of three parts which he considers to represent the similar, though distinct divisions present in *Varanus*. In the iguanines we have decided to treat the sternohyoideus complex as three separate muscles: sternohyoideus, sternothyroideus, and omohyoideus.

The sternohyoideus originates as several heads from the clavicle. Its oblique fibers extend anteriorly to insert on the posterior surface of the first ceratobranchial. In all the genera examined, the sternohyoideus forms a broad elongated sheet of muscle with the exception of *Ophurus* where its appearance is narrow and cordlike.

M. Omohyoideus

M. Omohyoideus (Figs. 11, 12, 15, 16, 25, and 26) is sheetlike, and forms the lateral extension of the sternohyoideus complex. In all genera examined it originates mesially from the lateral tip of the transverse process of the interclavicle with some fibers of the episternocleidomastoideus. Laterally, the omohyoideus takes its origin from the anterolateral surface

of the clavicle and anterior border of the suprascapula.

The fibers of the omohyoideus pass obliquely anterior to insert on the posterior margin of the first ceratobranchial and the proximal end of the second ceratobranchial cartilages.

In all of the iguanines examined except *Chalarodon*, the medial border is different to separate from the lateral border of the sternohyoideus. The delineation of both muscles must be made by comparing the origins and insertions. In *Chalarodon* the omohyoideus is easily separated as the fibers of this muscle pass oblique to those of the sternohyoideus.

M. Sternothyroideus

M. Sternothyroideus (Figs. 11 and 12) is the most medial extension of the sternohyoideus complex and can be separated from the other members of this muscle group by its different origin and insertion. The name sternothyroideus is used as in Camp (1923:451) who figured this muscle as the deep member of the complex in *Brachylophus*.

The origin of this muscle is considered to be those fibers that arise from the interclavicle and sternum. These fibers pass anteriorly and parallel to the trachea to insert on the hyoid at the point of union between the basihyal and the hypohyal.

In the genera examined the lateral border of the sternothyroideus and the medial border of the sternohyoideus are difficult to determine except in *Ophurus* and *Chalarodon* where the borders of both muscles are separated in situ.

Neck Musculature

M. Constrictor colli

M. Constrictor colli (Figs. 11, 12, 17, 18, 23 and 24), the most superficial muscle of the cervical region, is overlain by the connective tissue of the skin and a few scattered fat pads. The constrictor colli lies superficial to parts of the depressor mandibularis and episternocleidomastoideus, and is from one to two fibers thick.

The main origin of this muscle is on the superficial dorsolateral fascia of the neck which extends almost as far as the posterior margin of the depressor mandibularis. The muscle passes ventrolaterally posterior to the retroarticular process of the articular bone, and inserts on the extensive ventral aponeurosis at the midline, which also serves as the point of insertion for the intermandibularis posterior.

The relationships between the anterior border of the constrictor colli and the posterior border of the intermandibularis posterior have previously been described. The width of the constrictor colli is variable in the iguanines. The muscle is widest, covering most of the lateral surface of the neck, in *Amblyrhynchus*, *Chalarodon*, *Cychura*, *Iguana*, and *Sauromalus*.

malus. A narrow constrictor colli is found in *Brachylophus*, *Conolophus*, *Ctenosaura*, *Dipsosaurus*, and *Oplurus*.

M. Episternocleidomastoideus

M. Episternocleidomastoideus (Figs. 11, 12, 19, 20, 23, 24, 25, 26, 27 and 28) is a neck muscle crossing at an oblique angle from the shoulder to the head. It is overlain by the depressor mandibularis which covers its anterior end. The episternocleidomastoideus lies superficial to the omohyoideus, tympanic membrane, distal ends of the ceratohyal, ceratobranchial bones, and the two levator scapulae muscles.

The origin is a single head arising from the lateral process of the interclavicle. The insertion occurs on the distal half of the parietal crest, the lateral surface of the paraoccipital process of the exoccipital bone and with some connection to the fascia of the dorso-lateral angle of the neck.

This muscle was not found to deviate from this pattern in any of the specimens examined.

M. Depressor mandibularis

M. Depressor mandibularis (Figs. 17, 18, 23, 24, 25 and 26) is situated laterally with its anterior edge bordering the auditory meatus posteriorly. It is overlain by the constrictor colli. The anterior part of the depressor mandibularis is superficial to part of the posterior fibers of the adductor mandibularis externus medius and the posterior border of the tympanic membrane. Its posterior parts pass superficially to the anterior fibers of the trapezius and the episternocleidomastoideus, with some lying superficial to the distal ends of the ceratohyal, ceratobranchial bones and the tympanium.

The depressor mandibularis can be subdivided into three bundles. The origin of the anterior bundle is from the anterolateral surface of the posterolateral parietal wing and parietal crest. This bundle makes up the major part of the depressor mandibularis muscle and passes posteroventrally with a tendinous insertion on the retroarticular process of the articular bone.

The intermediate bundle, in its posterior region, originates from the fascia along the dorsolateral angle of the neck, in the region of the first cervical vertebrae, and ventral to the constrictor colli. This bundle has a common origin with the posterior bundle (cervicomandibularis) and a common insertion, ventrally, with fibers of the anterior bundle on the retroarticular process. The intermediate bundle is sheetlike rather than forming a thick mass as does the anterior and posterior bundle.

When distinct the posterior bundle is considered a separate muscle, the cervicomandibularis (Figs. 17, 18, 23, 24, 25, and 26). It is separable from the other two bundles at its insertion and throughout most of its length. It takes its origin from the superficial fascia

of the dorsal midline of the neck in common with the posterior fibers of the intermediate bundle, and ventral to the origin of the constrictor colli. It extends anteroventrally along the posterior border of the intermediate bundle and continues past the insertion of the anterior and intermediate bundles to insert on the superficial fascia of the intermandibularis and the skin.

Some variations in the width of the anterior bundles occur in *Iguana* and *Conolophus* where the bundle is very narrow and in *Amblyrhynchus* where the bundle is thick and wide.

The cervicomandibularis also shows considerable variation in distinctness and relationship to the origin of the constrictor colli. Robison and Tanner (1962:8) indicate that this posterior bundle became indistinct in old forms of *Crotaphytus*. The problem of distinctness may be a function of age. Unfortunately the small sample sizes used in this study can lend no support to that theory.

In *Brachylophus*, *Chalarodon* and *Dipsosaurus*, the cervicomandibularis is extensive and its posterior border at the origin extends posteriorly beyond the posterior border of the origin of the constrictor colli, thereby making the cervicomandibularis the most superficial muscle, at its origin in that area of the neck. In all other genera examined, the cervicomandibularis is completely obscured by the more superficial constrictor colli.

M. Levator scapulae superficialis

M. Levator scapulae superficialis (Figs. 17, 18, 19, 20, 25, 26, 27, 28, 29 and 30) is normally considered to be a muscle of the pectoral girdle. Inasmuch as it originates on the neck, deep to the neck musculature it will be included with these muscles.

The levator scapulae superficialis is a broad fan-shaped muscle, lying mostly anterior, but partly superficial to the suprascapula bone. It is superficial to the levator scapulae profundus, the axial musculature and the posterodorsal fibers of the origin of the omohyoideus.

The constrictor colli, trapezius, episternocleidomastoideus, depressor mandibularis, tympanic membrane, distal ends of the ceratohyal and the first ceratobranchial all contribute to the superficial layer over this muscle.

The origin of the levator scapulae superficialis is in a tendon, common to it and the levator scapulae profundus. The tendon is attached to the diapophysis of the atlas. The muscle extends posterodorsally and inserts on the anterior half of the lateral surface of the scapula. There is little deviation in this pattern in the genera examined.

M. Levator scapulae profundus

M. Levator scapulae profundus (Figs. 19, 20, 27, 28, 29 and 30) is the deep partner of the levator

scapulae superficialis, and has a similar position with relation to the surrounding muscles, with the exception that the posterior fibers of insertion pass deep to those of the omohyoideus muscle.

The origin is by a common tendon with the levator scapulae superficialis, from the diapophysis of the atlas. Muscle fibers pass posterodorsally to insert along the anterior margin of the suprascapula just ventral to the insertion of the levator scapulae superficialis, and to the anterior surface of the acromial end of the clavicle.

Temporal Musculature

M. Pterygomandibularis

M. Pterygomandibularis (Figs. 11, 12, 13, 14, 15 and 16) is a large muscle at the angle of the jaw covering a large part of the posterior half of the mandible. It reaches its largest size between the mandibular rami and lateral to the trachea. The intermandibularis posterior lies superficial to it laterally with the oral membrane bordering it ventromesially. The third mandibulo-hyoideus and the hyoglossus lie ventral to it.

The origin of the pterygomandibularis is in a heavy tendon arising from the ventral projection of the ectopterygoid, and the transverse process of the pterygoid. Some fibers also originate as a tendonous sheath from the remaining part of the transverse process, and the ventrolateral border of the quadrate process of the pterygoid with part from the ventral border of the basiptyergoid process of the basisphenoid bone where this bone articulates with the pterygoid.

The main fibers of this muscle extend posteriorly and posterodorsally, to obscure the ventral and lateral surfaces of the angular, articular, and surangular bones of the mandible. The fibers insert on the dorsal, mesial, and ventral surfaces of the articular bone, including the retroarticular and angular processes. Some fibers form a line across the lateral surface of the angular and the surangular foramen. Between the foramen and the adductor mandibularis externus superficialis, a tendonous insertion extends lengthwise through the muscle mass in a posterior direction and attaches to the angular process of the articular.

M. Levator angularis oris

M. Levator angularis oris (Figs. 23 and 24), the most superficial muscle of the infratemporal fossa, is overlain by the infratemporal fascia and the skin. It covers part of the surface of the adductor mandibularis externus superficialis.

It is this muscle which arises from the mesial surfaces of the superficial infratemporal fascia, the ventrolateral surfaces of the squamosal, the posterior part of the jugal, and the anterodorsal angle of the tympanic crest. The fibers pass anteroventrally to insert near the posterior border of the coronoid.

The size of the levator angularis oris differs in the genera examined. In all of the genera except *Brachylophus* and *Dipsosaurus*, the muscle covers over half the infratemporal fossa. In *Brachylophus* and *Dipsosaurus* the muscle is small and narrow, covering less than a third of the anterior part of the infratemporal fossa.

M. Adductor mandibularis externus superficialis

M. Adductor mandibularis externus superficialis (Figs. 23, 24, 25 and 26), of the infratemporal fossa, is an extensive muscle mass which mesially is scarcely distinguishable from the adductor mandibularis externus medius. It lies beneath the levator angularis oris at its anterior border and beneath the superficial infratemporal fossa at its posterior border.

The superficialis originates from the ventral surface of the postorbital, squamosal, jugal and quadrate bones, and from the lateral surfaces of the tympanic crest. The fibers, which extend anteroventrally, are more ventrally oriented than those of the levator angularis oris. They insert along the beveled, dorso-lateral surface of the supra-angular, with fibers passing dorsal to the posterior supra-angular foramen and covering the anterior surangular foramen. The most anterior of these fibers insert on the lateral and posterolateral surface of the coronoid with parts inserting on the lateral surfaces of the bodenaponeurosis.

M. Adductor mandibularis externus medius

M. Adductor mandibularis externus medius (Figs. 17, 18, 23, 24, 25, 26, 27 and 28) is a large muscle, faintly separated from and mesial to the adductor mandibularis externus superficialis and dorsolateral to the adductor mandibularis externus profundus. It is also posterolateral to the pseudotemporalis superficialis with the exception of its anteromesial fibers which are dorsal to that muscle. The origin of this muscle is from the mesial surface of the squamosal, the anterolateral surfaces of the supratemporal and the posterolateral wing of the parietal, the dorsolaterally beveled surface of the parietal, and from the anterior and dorsal surfaces of the quadrate bone. Fibers extend anteroventrally with the dorsal ones being more anteriorly oriented than the ventral. These insert along the dorsomesial surface of the surangular, the posterior surface of the coronoid, and the lateral, posterior, and mesial sides of the bodenaponeurosis.

M. Adductor mandibularis externus profundus

M. Adductor mandibularis externus profundus (Figs. 29 and 30), a massive muscle, not clearly separable from the adductor mandibularis externus medius, is located ventrolaterally to the pseudotemporalis superficialis, dorsal to the prootic, and lateral

to the braincase and the supraoccipital.

This muscle's origin arises from the entire postero-mesial border of the posterolateral wing of the parietal, from the paraoccipital process of the exoccipital, and from the dorsolateral surface of the posterior process of the prootic bone. From its parietal origin this muscle turns ventrally and anteroventrally to enter the infratemporal fossa where it passes ventral to the supratemporal and the posterolateral parietal wing and dorsal to the exoccipital and the posterior process of the prootic bone. At this point it joins with another head from the prootic and continues anteroventrally to insert by the bodenaponeurosis on the posterior surface and base of the coronoid.

The adductor mandibularis externus group has been considered as a single mass (Adams, 1919) with separate slips as described above. According to Oelrich (1956:41) this group is divided into three muscles on the basis of its relations to the three rami of the trigeminal nerve. This system has been followed here for the sake of convenience and clarity. No special differences were noted in the genera examined.

M. Pseudotemporalis superficialis

M. Pseudotemporalis superficialis (Figs. 17, 18, 29, and 30) is a divergent, massive muscle with a complex placement. It lies ventromesial to the adductor mandibularis externus medius, posterior to the orbit, anterolateral to the cranial cavity, lateral to the epipterygoid, and lateral to the pseudotemporalis profundus. The posterior fibers are trapped between the adductor mandibularis externus profundus and the adductor mandibularis externus medius.

The origin of the pseudotemporalis superficialis is from the dorsolaterally beveled lateral margin of the parietal, part of the anterolateral surface of the parie-

tal wing, the lateral surfaces of the anterior semicircular canal, and the alar process of the prootic, and the internal surface of the dorsal one-third of the epipterygoid. Fibers of the anterior part pass ventrally while posterior fibers extend anteroventrally. The insertion is with the pseudotemporalis profundus, on the mesial surface of the bodenaponeurosis, the posteromesial border of the coronoid to its base and the dorsal border of the articular to its midpoint.

M. Pseudotemporalis profundus

M. Pseudotemporalis profundus (Figs. 31 and 32), a pyramid shaped muscle, lies just posteromesial to the pseudotemporalis superficialis, lateral to the epipterygoid bone and the levator pterygoideus muscle.

This muscle arises from the anterior, lateral, and posterior sides of the ventral two-thirds of the epipterygoid bone. These fibers extend ventrally to insert with the pseudotemporalis superficialis muscle, on the posteromesial border of the coronoid bone and on the dorsal surface of the articular bone to its midpoint.

M. Adductor mandibularis posterior

M. Adductor mandibularis posterior (Figs. 31 and 32) is a wide straplike muscle, lying lateral to the tympanic cavity, the protractor pterygoideus muscle, and mesial to the mandible and to the adductor mandibularis externus muscles.

A few fibers arise from the lateral and mesial surfaces of an aponeurosis running between the mesial crest of the quadrate and Meckel's cartilage. Other fibers take their origin from the posterior process of the prootic bone. All fibers pass anteroventrally to insert with some fibers of the pseudotemporalis muscles on the dorsal surface of the articular bone, and on Meckel's cartilage.

TABLE 35
SUMMARY OF IMPORTANT MYOLOGICAL DIFFERENCES

Genus	Intermandibularis Posterior, position of posterior border		Sternothyroideus lateral border		Constrictor Colli Width		Cervicomandibularis		Levator Angularis Oris	
	Free	Connected	Separate	Attached	Wide	Narrow	Visible	Hidden	Large	Small
<i>Amblyrhynchus</i>		X		X	X			X	X	
<i>Brachylophus</i>		X		X		X	X			X
<i>Chalarodon</i>		X	X		X		X		X	
<i>Conolophus</i>	X			X		X		X	X	
<i>Ctenosaura</i>	X			X		X		X	X	
<i>Cyclura</i>	X			X	X			X	X	
<i>Dipsosaurus</i>		X		X		X	X			X
<i>Iguana</i>		X		X	X			X	X	
<i>Oplurus</i>		X	X			X		X	X	
<i>Sauromalus</i>	X			X	X			X	X	

M. Levator pterygoideus

M. Levator pterygoideus (Figs. 31, 32, 33, and 34), a triangular shaped muscle, lies posteromesial to the epipterygoid bone and the pseudotemporalis profundus muscle. It lies anterolateral to the protractor pterygoideus and lateral to the prootic membrane of the cranial cavity.

The origin is by a flat tendon from the ventral surface of the parietal bone, mesial to the epipterygoid, and posteriorly along the lateral margin of the parietal to its midpoint. Some fibers fan out posteroventrally to insert, with anterior fibers of the protractor pterygoideus, on the proximal dorsal surface of the quadrate process of the pterygoid bone, beginning posterolateral to the fossa columella and extending anteromesially, to end mesial to the epipterygoid.

M. Protractor pterygoideus

M. Protractor pterygoideus (Fig. 31, 32, 33, and

34), a broad, short muscle, which forms the anterolateral wall of the tympanic cavity. This muscle lies posteromesial to the levator pterygoideus and lateral to the basisphenoid bone, and the anterior parts of the prootic bone.

The origin of this muscle is from the lateral surface of the anterior inferior process of the prootic bone, the posteroventral end of the pila antotica, and from a tendon which comes from the anterior inferior process of the prootic to the region of the condyle on the anterior tip of the basiptyergoid process of the basisphenoid bone. Most fibers of the protractor pterygoideus fan out, posteroventrally, to insert on the dorsal and mesial crest of the quadrate. Some anterior fibers insert with those of the levator pterygoideus. The majority remain posteromesial to this muscle.

OTHER CHARACTERS

Besides the osteology and myology, the structure of the tongue and hemipenes of iguanine lizards has been investigated.

Tongue

Only one tongue from each genus was examined with the exception of *Dipsosaurus*, where three tongues were utilized. Measurements were taken of total length, measured from the anterior tip to the most posterior extension of the tongue. Width was recorded as the greatest distance, at a right angle, to the length. Width in all cases was taken at the most posterior extremities of the tongue which is the widest region. The depth of both anterior and posterior indentation or clefts was also measured. Ratios were computed between length and width, length and depth of anterior cleft, and length and depth of posterior cleft.

The tongues (Figure 35) in all the iguanines are fleshy and protrusible with an arrowhead shape, a slight cleft anteriorly and a deeper cleft posteriorly, which surrounds the glottis laterally. The tongue is covered with "...velvety filamentous papillae..." (Oelrich, 1956:53) which are missing or very small at the most anterior tip and become increasingly larger posteriorly until, at the posterior extremity of the tongue, the papillae are fleshy and pointed rather than blunt.

As table 36 shows, the most elongated and narrow tongues are those of *Ctenosaura* (length times width ratio .491), *Sauromalus* (.530) and *Cychura* (.539). The fattest tongues are found in *Chalarodon* (.705), *Dipsosaurus* (.698), and *Ophurus* (.691). The other genera show an intermediate situation for this character.

The deepest anterior cleft is found in *Dipsosaurus* (length times depth of anterior cleft .147), *Ophurus* (.119) and *Ctenosaura* (.118). The shallowest clefts are those possessed by *Cychura* (.036), *Brachylophus* (.039), and *Amblyrhynchus* (.044).

The posterior cleft is deepest in *Cychura* (length times depth of posterior cleft ratio .369) and *Ctenosaura* (.368). The shallowest posterior cleft is found in *Conolophus* (.239), *Ophurus* (.245), and *Chalarodon* (.279). All other genera are intermediate between these two extremes.

The anterior tip of the tongue is free of papillae in all genera examined except *Ctenosaura*. Oelrich (1956:53) also found the dorsum of the tongue in *Ctenosaura* to be completely covered.

The development of the fleshy pointed papillae at the posterior of the tongue is extensive in all of the genera except *Chalarodon* and *Ophurus* where the papillae are poorly developed and few in number.

TABLE 36
TONGUE MEASUREMENTS

Genus	Length	Width	Anterior Cleft	Posterior Cleft	Length Width Ratio	Length Ant. Cleft Ratio	Length Post. Cleft Ratio
<i>Amblyrhynchus</i>	33.7	19.3	1.5	9.8	.572	.044	.290
<i>Brachylophus</i>	20.1	11.5	0.8	5.8	.572	.039	.288
<i>Chalarodon</i>	6.8	4.8	0.4	1.9	.705	.058	.279
<i>Conolophus</i>	37.1	22.4	2.4	8.9	.604	.064	.239
<i>Ctenosaura</i>	24.4	12.0	2.8	9.0	.491	.118	.368
<i>Cychura</i>	16.5	8.9	0.6	6.1	.539	.036	.369
<i>Dipsosaurus</i>	11.5	8.0	1.7	3.6	.698	.147	.318
<i>Iguana</i>	28.6	16.0	1.4	8.4	.559	.049	.293
<i>Ophurus</i>	15.9	11.0	1.9	3.9	.691	.119	.245
<i>Sauromalus</i>	19.8	10.5	1.4	5.8	.530	.070	.291

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
C. *Chalarodon madagascariensis*. BYU 22801, 22803. $\times 3.0$
D. *Conolophus subcristatus*. BYU 22811. $\times 10.35$
E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 11.

- cc-constrictor colli
ep-episternocleidomastoideus
g-genioglossus
iap-intermandibularis anterior profundus
ias-intermandibularis anterior superficialis
ip-intermandibularis posterior
mhl-mandibulohyoideus I
myH-mandibulohyoideus II
om-omohyoideus
pe-pectoralis
pt-ptyergomandibularis
sh-sternohyoideus
st-sternothyroideus

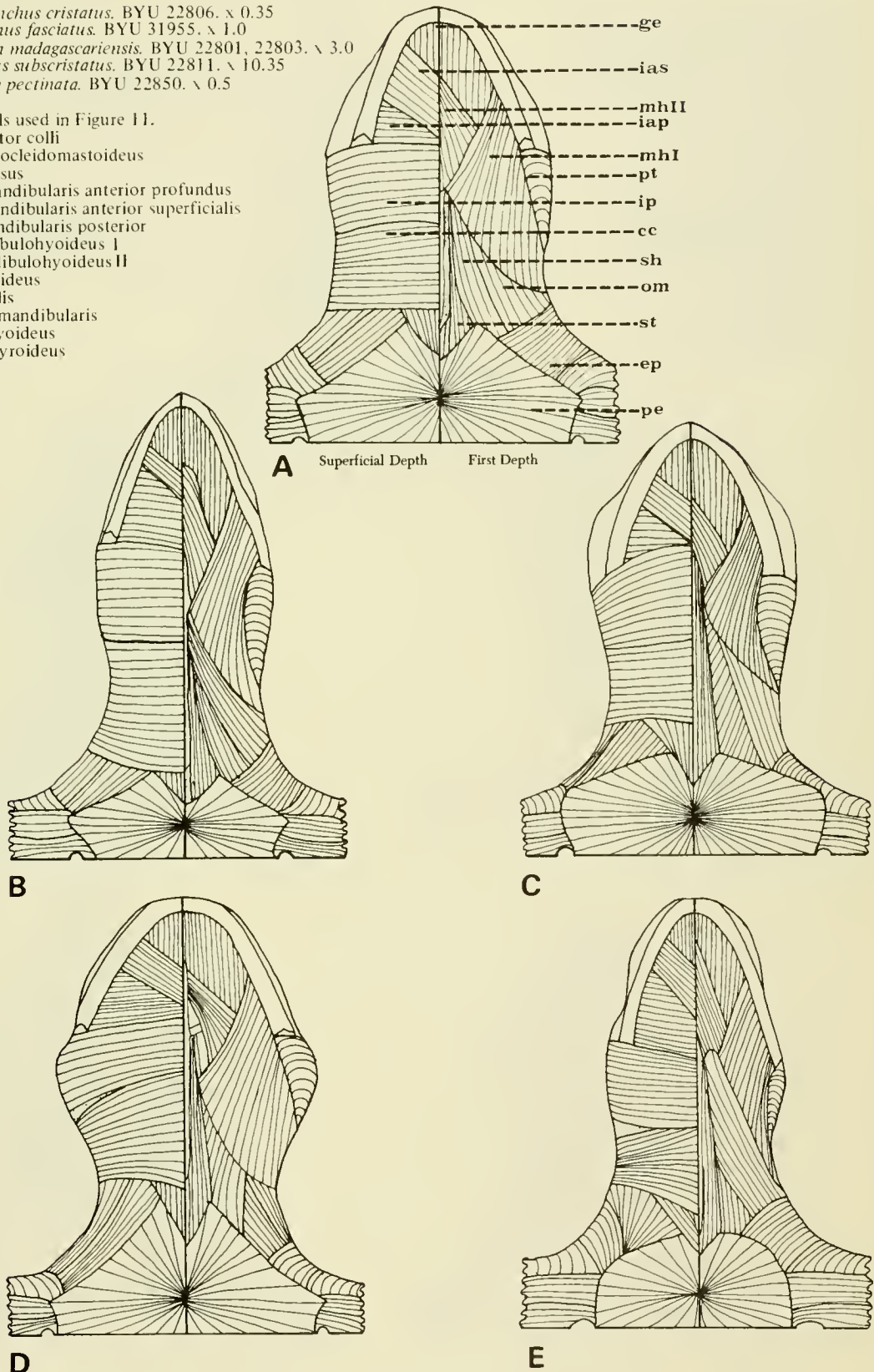


Figure 11. Ventral view of throat musculature; superficial layer shown at left and first depth at right.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
C. *Iguana iguana*. BYU 22851. $\times 0.75$
D. *Oplurus sebae*. BYU 11504. $\times 1.25$
E. *Sauromatus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 12.

- ce-constrictor colli
ep-episternocleidomastoideus
ge-genioglossus
iap-intermandibularis anterior profundus
ias-intermandibularis anterior superficialis
ip-intermandibularis posterior
mhl-mandibulohyoideus I
myII-mandibulohyoideus II
om-omohyoideus
pe-pectoralis
pt-ptyergomandibularis
sh-sternohyoideus
st-sternothyroideus

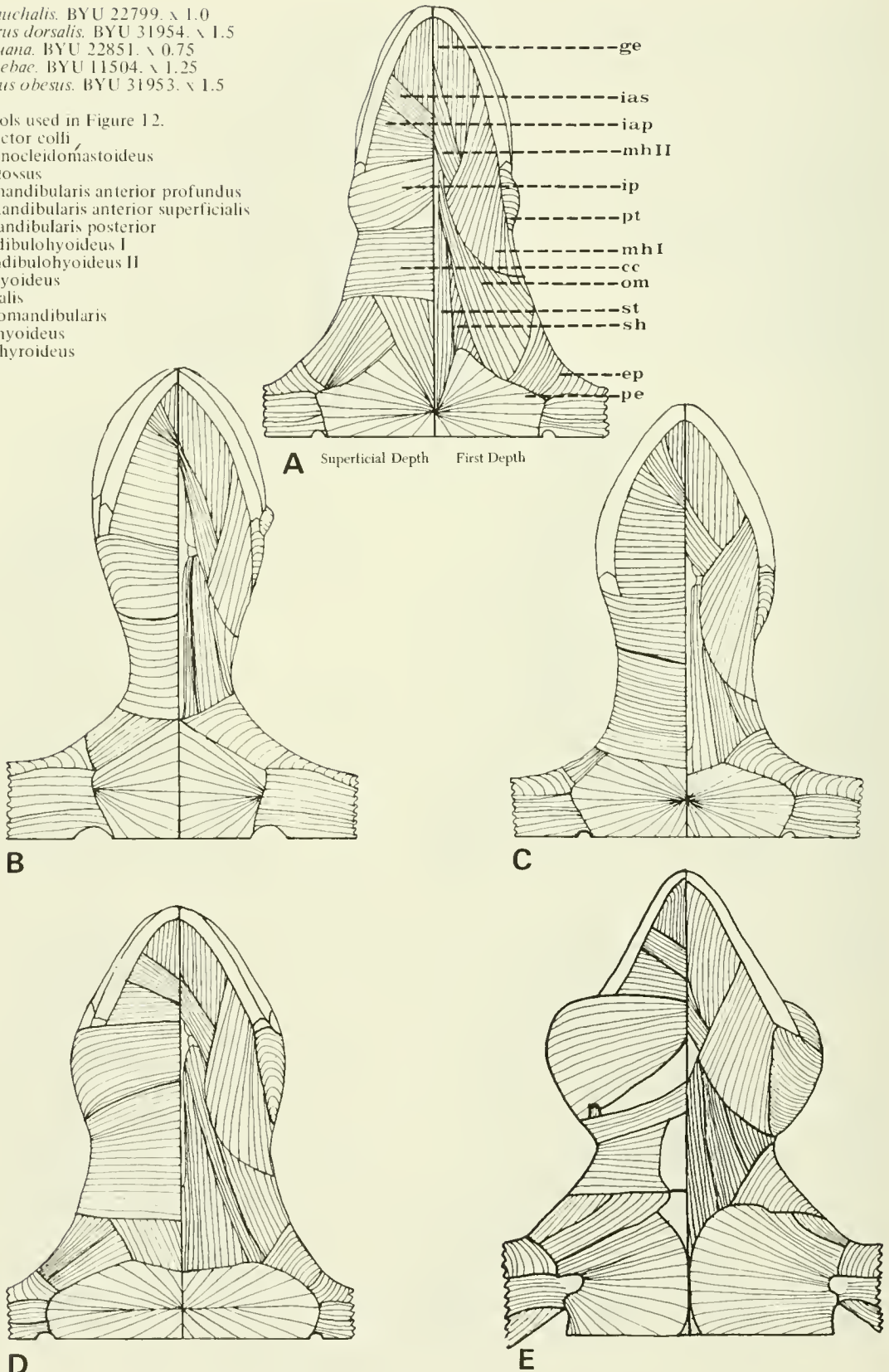


Figure 12. Ventral view of throat musculature; superficial layer shown at left and first depth at right.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
C. *Chalarodon madagascariensis*. BYU 22801, 22803. $\times 3.0$
D. *Conolophus subcristatus*. BYU 22811. $\times 0.35$
E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 13.
bh-branchiohyoideus
ge-genioglossus
hg-hyoglossus
mhIII-mandibulohyoideus III
pm-pharyngeal membrane
pt-ptyergomandibularis
sh-sternohyoideus

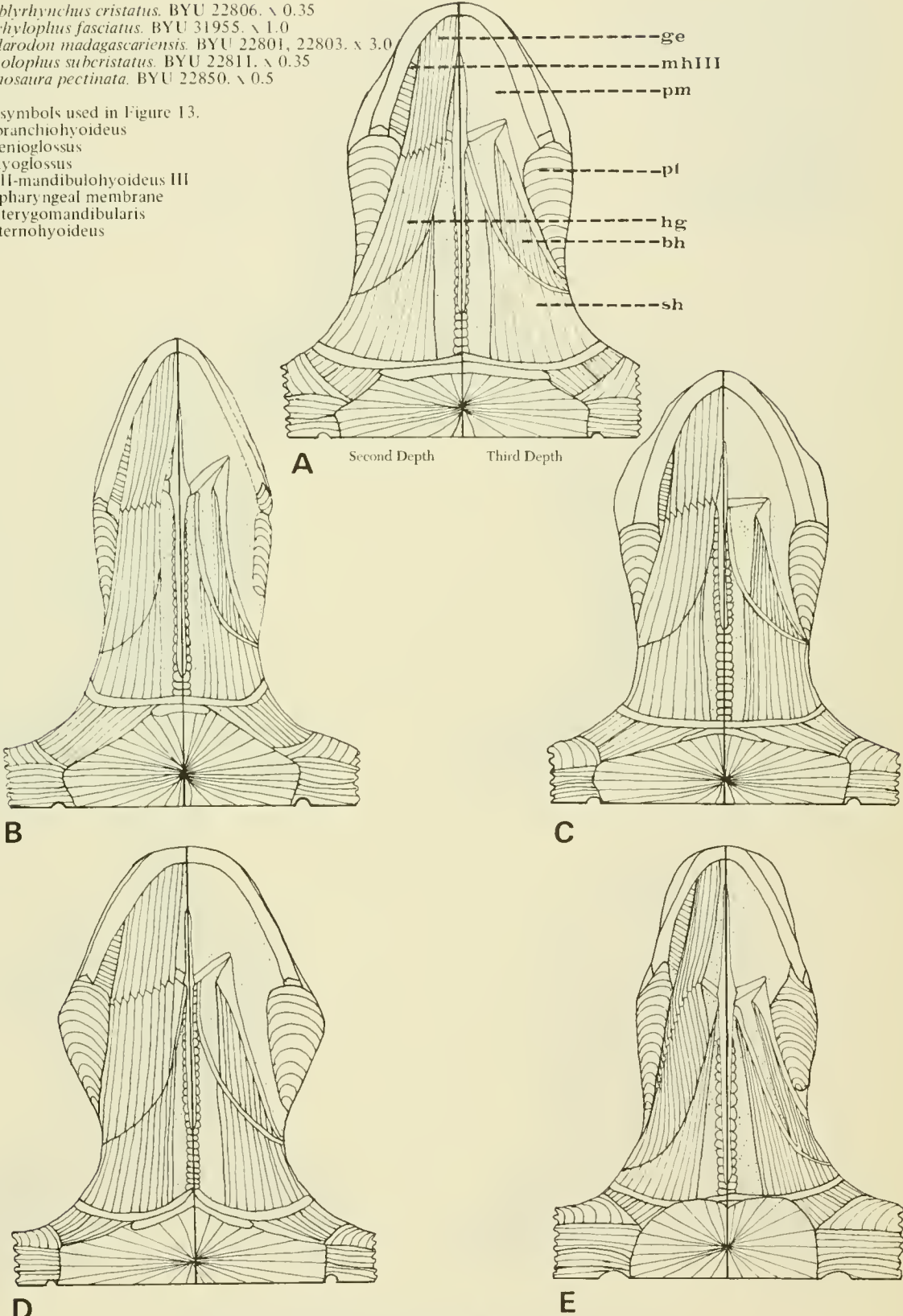


Figure 13. Ventral view of throat musculature; second depth at left and third depth at right.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 22851. $\times 10.75$
 D. *Oplurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 14.

bh-branchiohyoideus
 ge-genioglossus
 hg-hyglossus
 myIII-mandibulohyoideus III
 pm-pharyngeal membrane
 pt-ptyergomandibularis
 sh-sternohyoideus

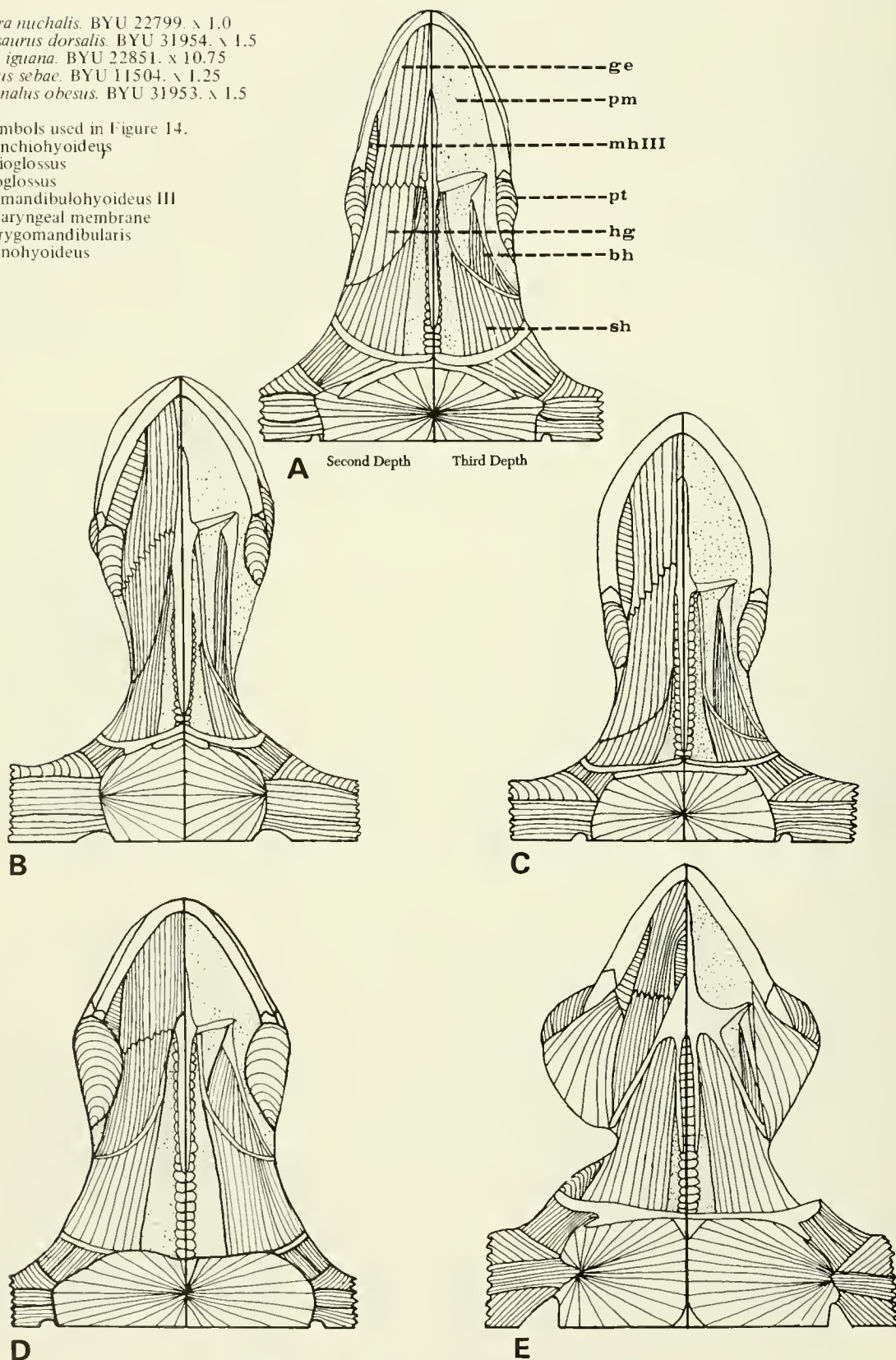


Figure 14. Ventral view of throat musculature; second depth at left and third depth at right.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
 B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
 C. *Chalarodon madagascariensis*. BYU 22801, 22803. $\times 3.0$
 D. *Conolophus subseriatus*. BYU 22811. $\times 10.35$
 E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 15.

cl-clavicle
 ic-interclavicle
 lx-larynx
 om-omohyoideus
 pm-pharyngeal membrane
 pt-ptyergomandibularis
 tr-trachea

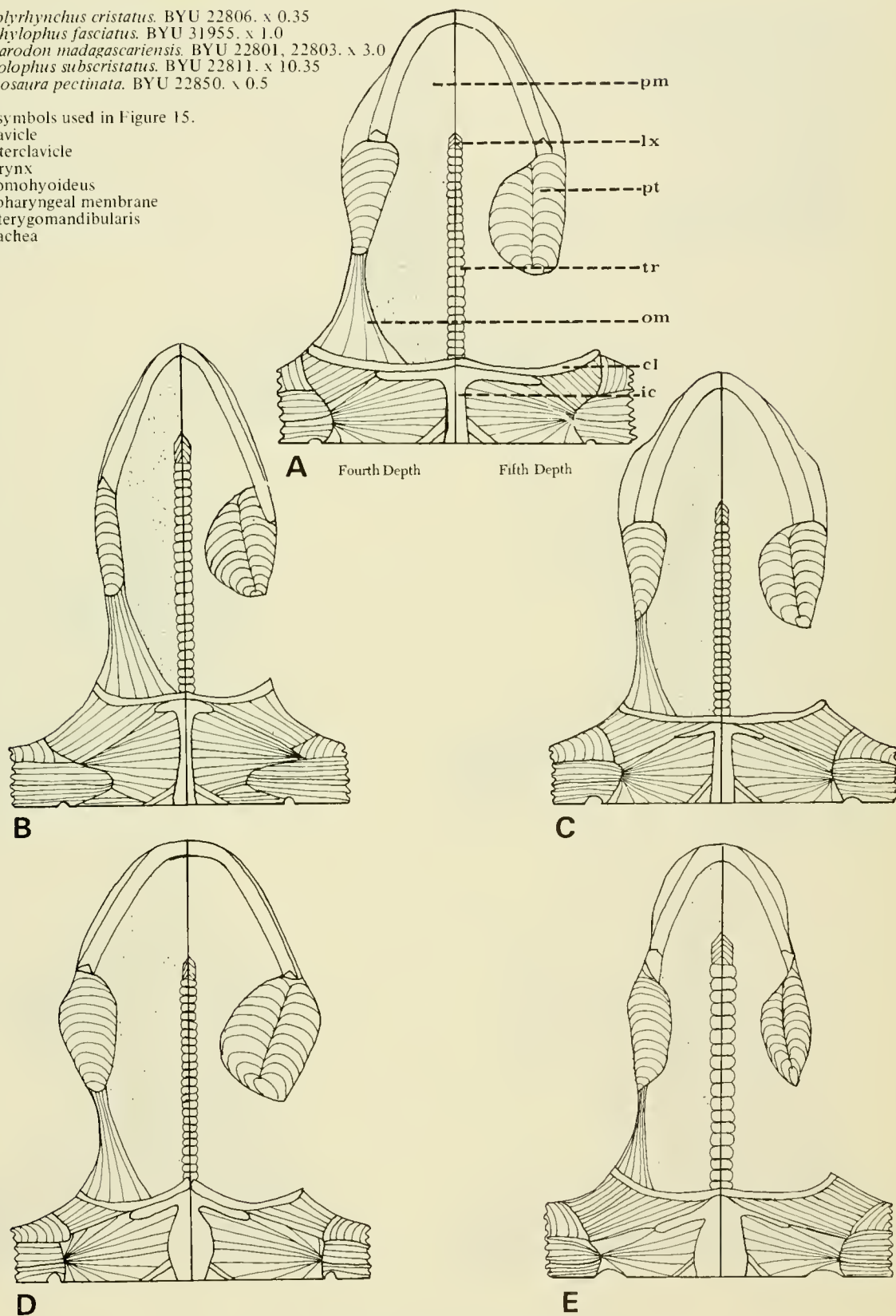


Figure 15. Ventral view of throat musculature; fourth depth at left and fifth depth at right.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 22851. $\times 0.75$
 D. *Oplurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 15.

cl-clavicle
 ic-interclavicle
 lx-larynx
 om-omohyoideus
 pm-pharyngeal membrane
 pt-ptyergomandibularis
 tr-trachea

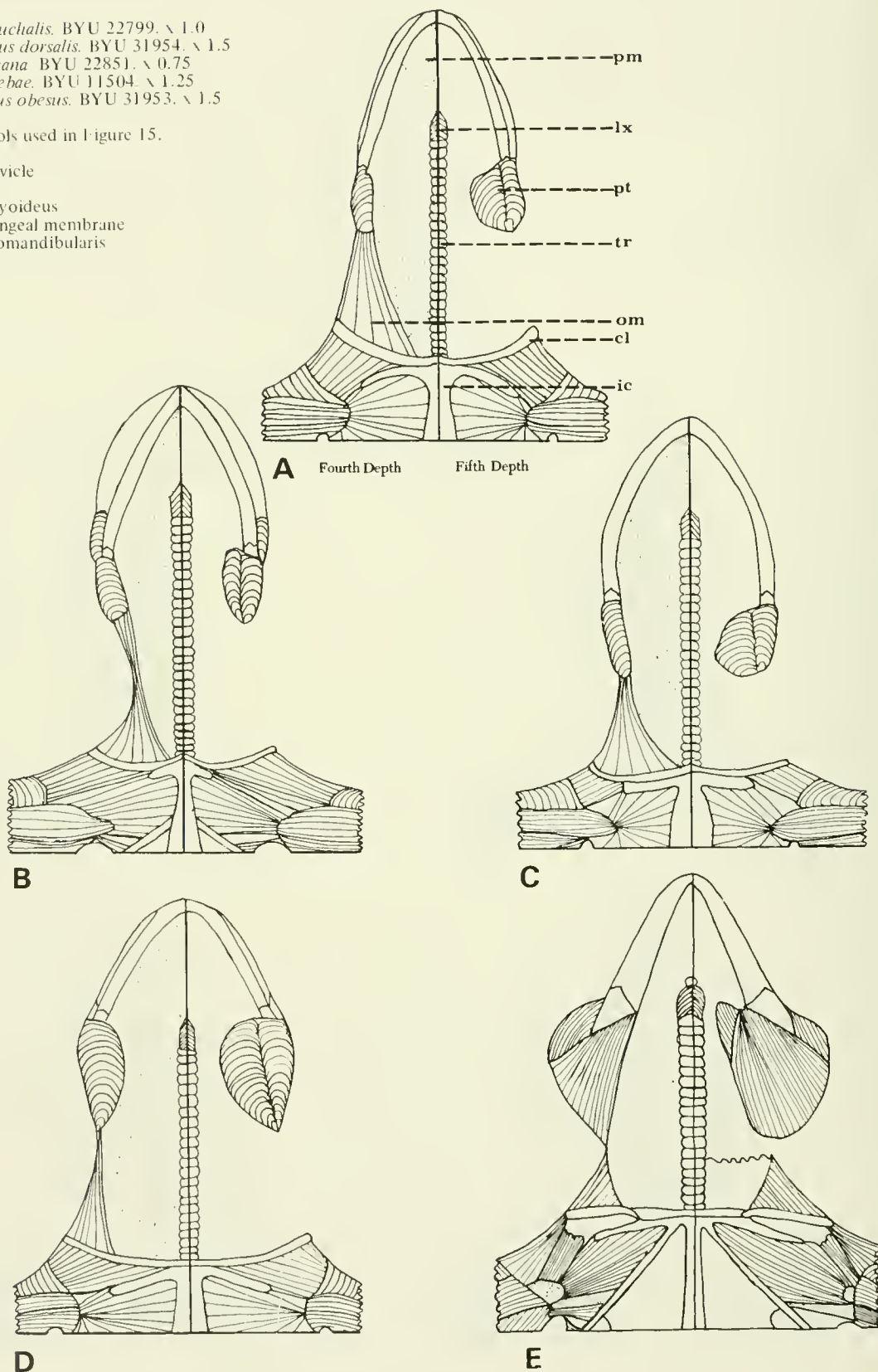


Figure 16. Ventral view of throat musculature; fourth depth at left and fifth depth at right.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
C. *Chalarodon madagascariensis*. BYU 22801, 22803. $\times 3.0$
D. *Conolophus suberistatus*. BYU 22811. $\times 0.35$
E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 17.
am-adductor mandibularis externus medius
cc-constrictor colli
cm-cervicomandibularis
dm-depressor mandibularis
ld-latissimus dorsi
ls-levator scapulae superficialis
ps-pseudotemporalis superficialis
tr-trapezius

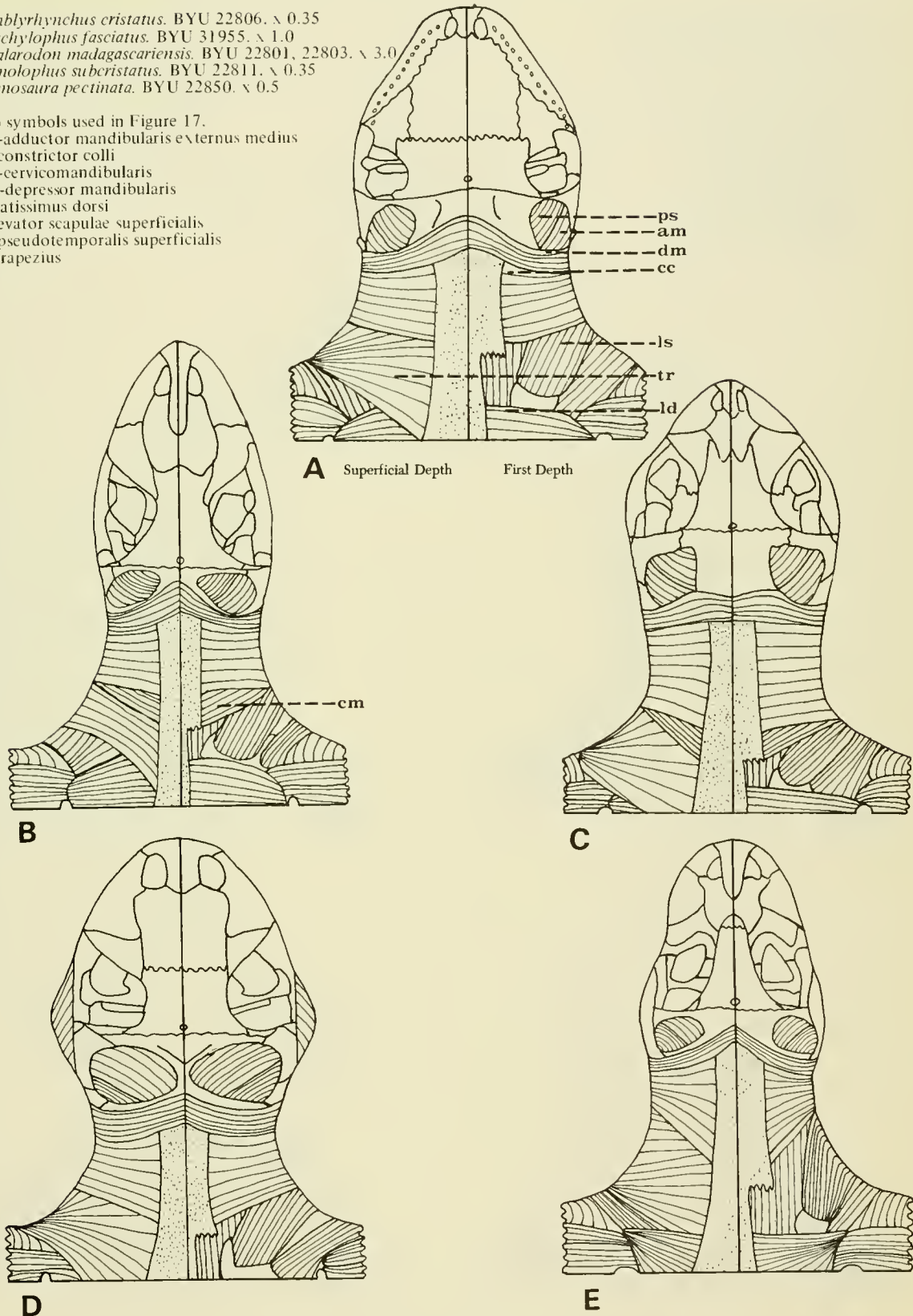


Figure 17. Dorsal view of head and neck musculature; superficial depth at left and first depth at right.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 22851. $\times 0.75$
 D. *Ophurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 18.

am-adductor mandibularis externus medius
 cc-constrictor colli
 cm-cervicomandibularis
 dm-depressor mandibularis
 ld-latissimus dorsi
 ls-levator scapulae superficialis
 ps-pseudotemporalis superficialis
 tr-trapezius

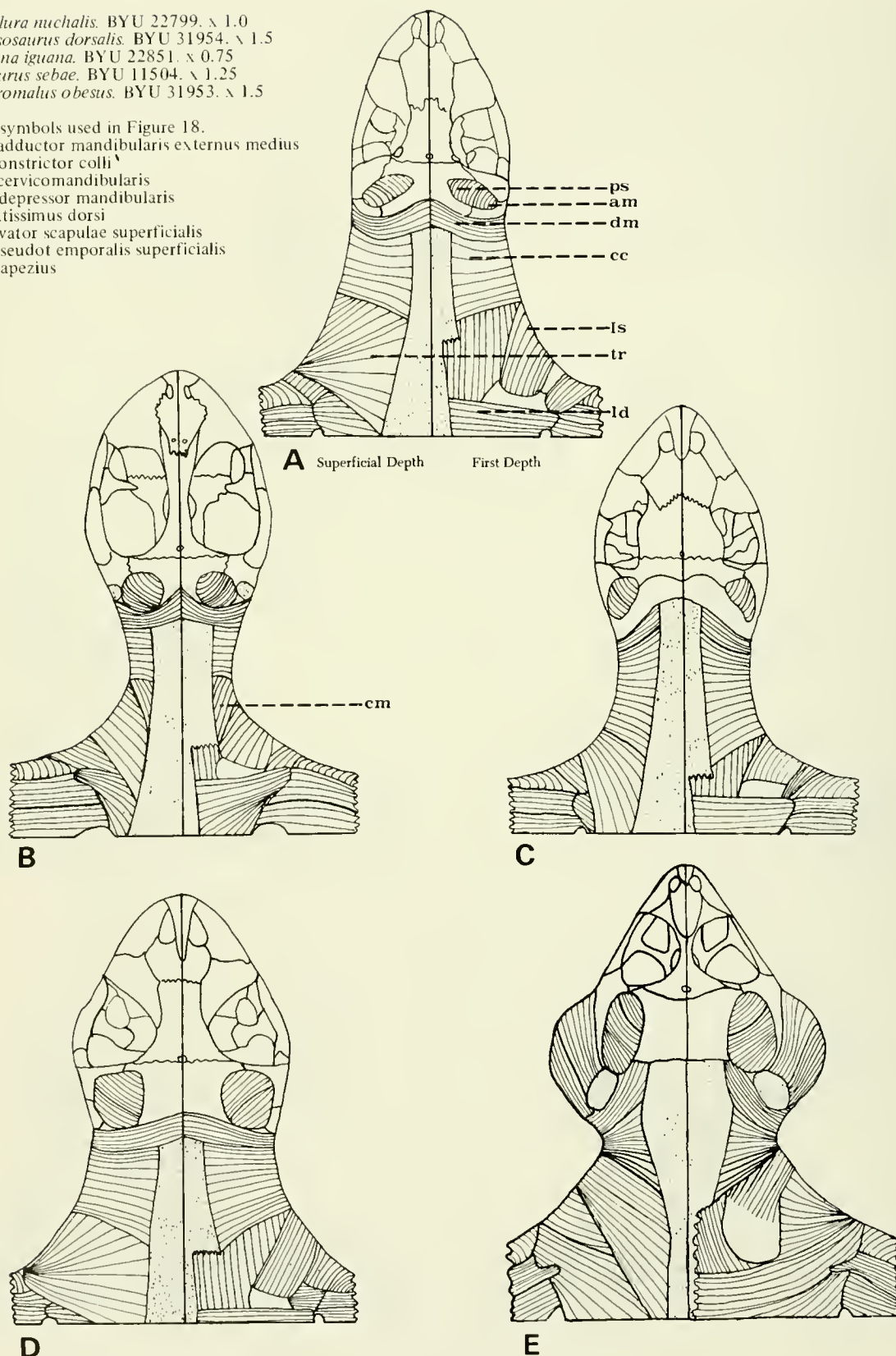


Figure 18. Dorsal view of head and neck musculature; superficial depth at left and first depth at right.

- A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 0.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 19.
ep-episternocleidomastoideus
lp-levator scapulae profundus
ls-levator scapulae superficialis
sd-serratus (dorsal part)
sl-sacrolumbalis

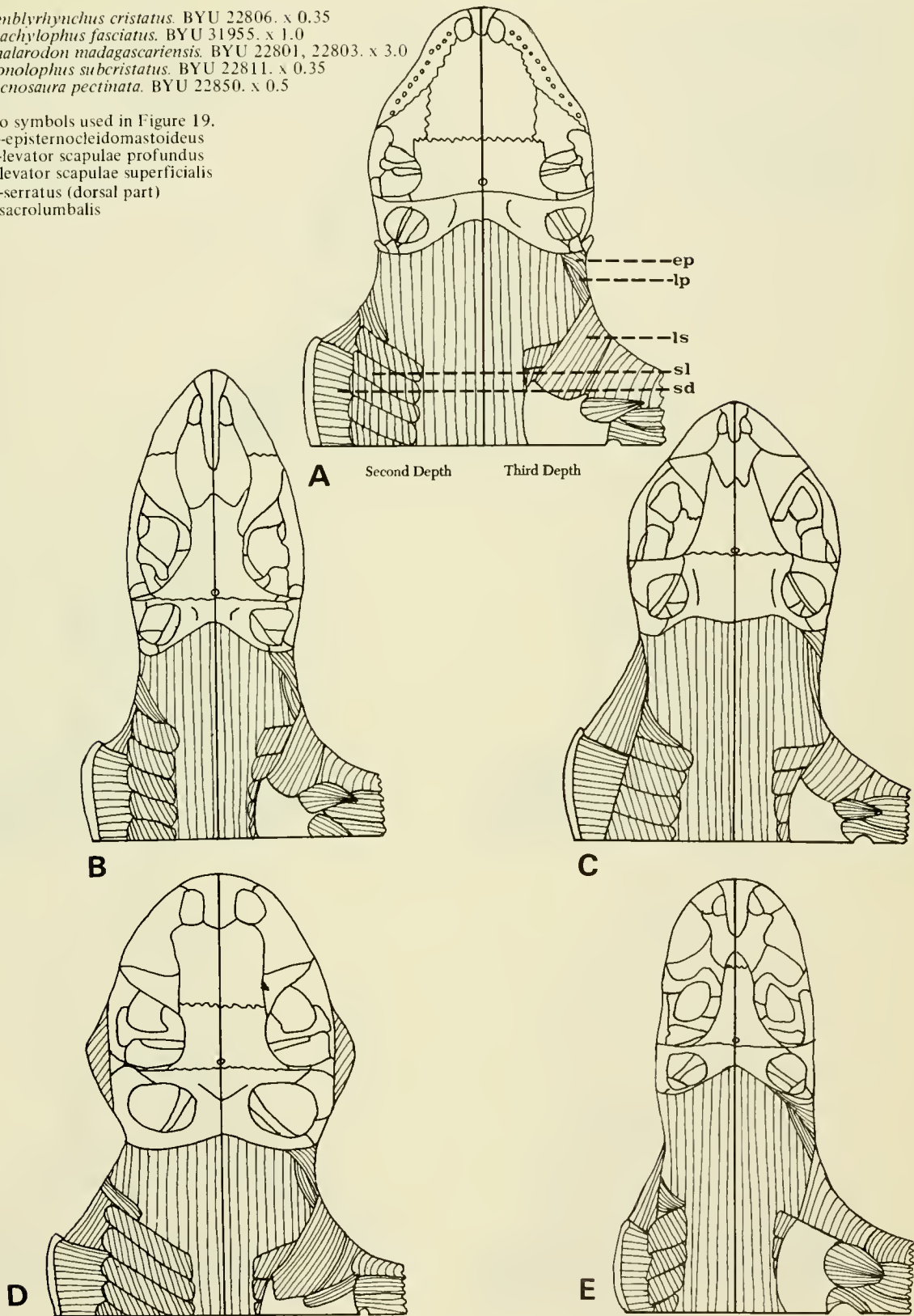


Figure 19. Dorsal view of head and neck musculature; second depth at the left and third depth at the right.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 22851. $\times 0.75$
 D. *Ophurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 20.
 ep-episternocleidomastoideus
 lp-levator scapulae profundus
 ls-levator scapulae superficialis
 sd-serratus (dorsal part)
 sl-sacrolumbalis

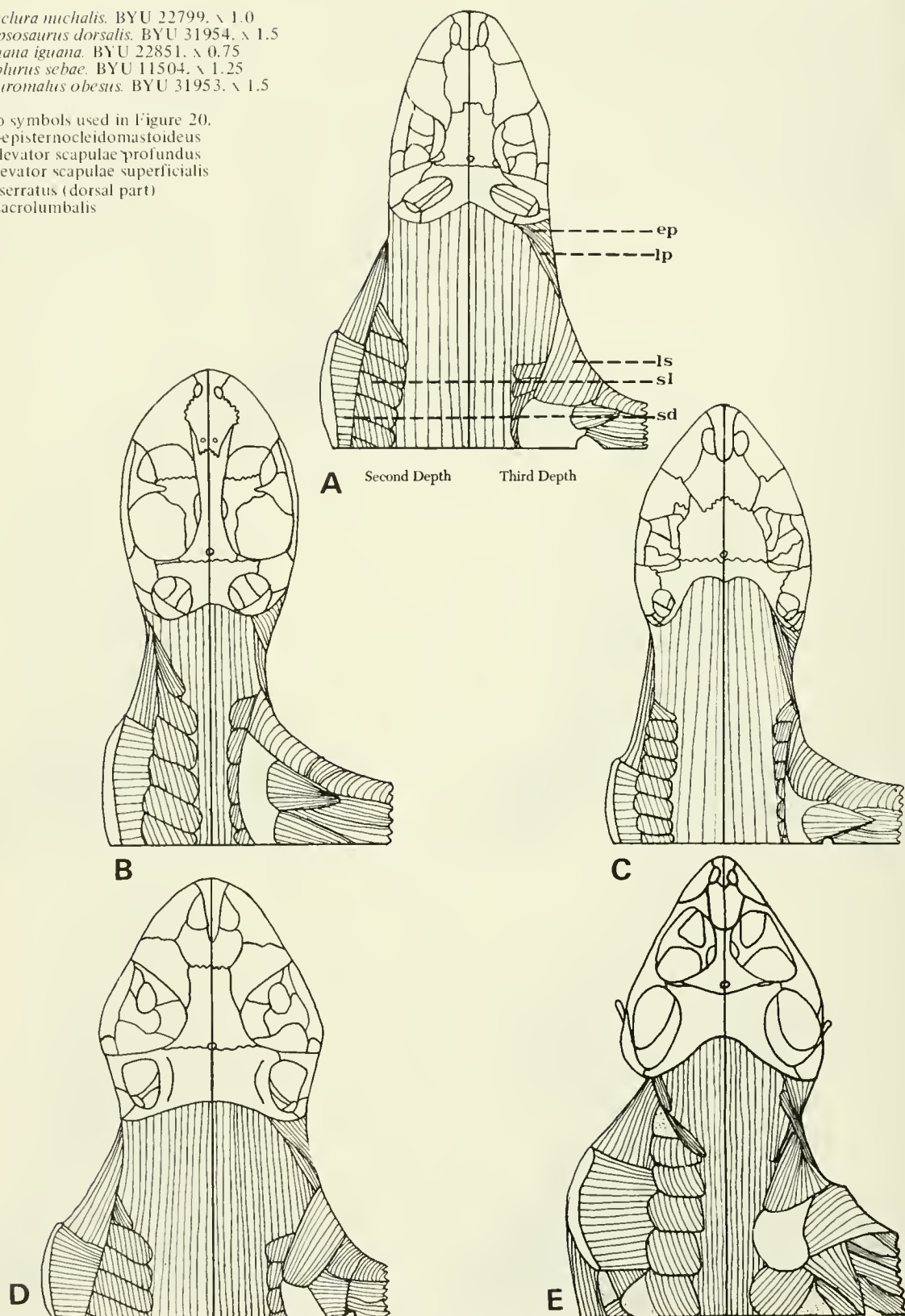


Figure 20. Dorsal view of head and neck musculature; second depth at the left and third depth at the right.

- A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
- B. *Brachylophus fasciatus*. BYU 31955. x 1.0
- C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
- D. *Conolophus subcristatus*. BYU 22811. x 0.35
- E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 21.
ie-intercostales externi
sd-serratus (dorsal part)
sp-spinus dorsi
ss-subscapularis II

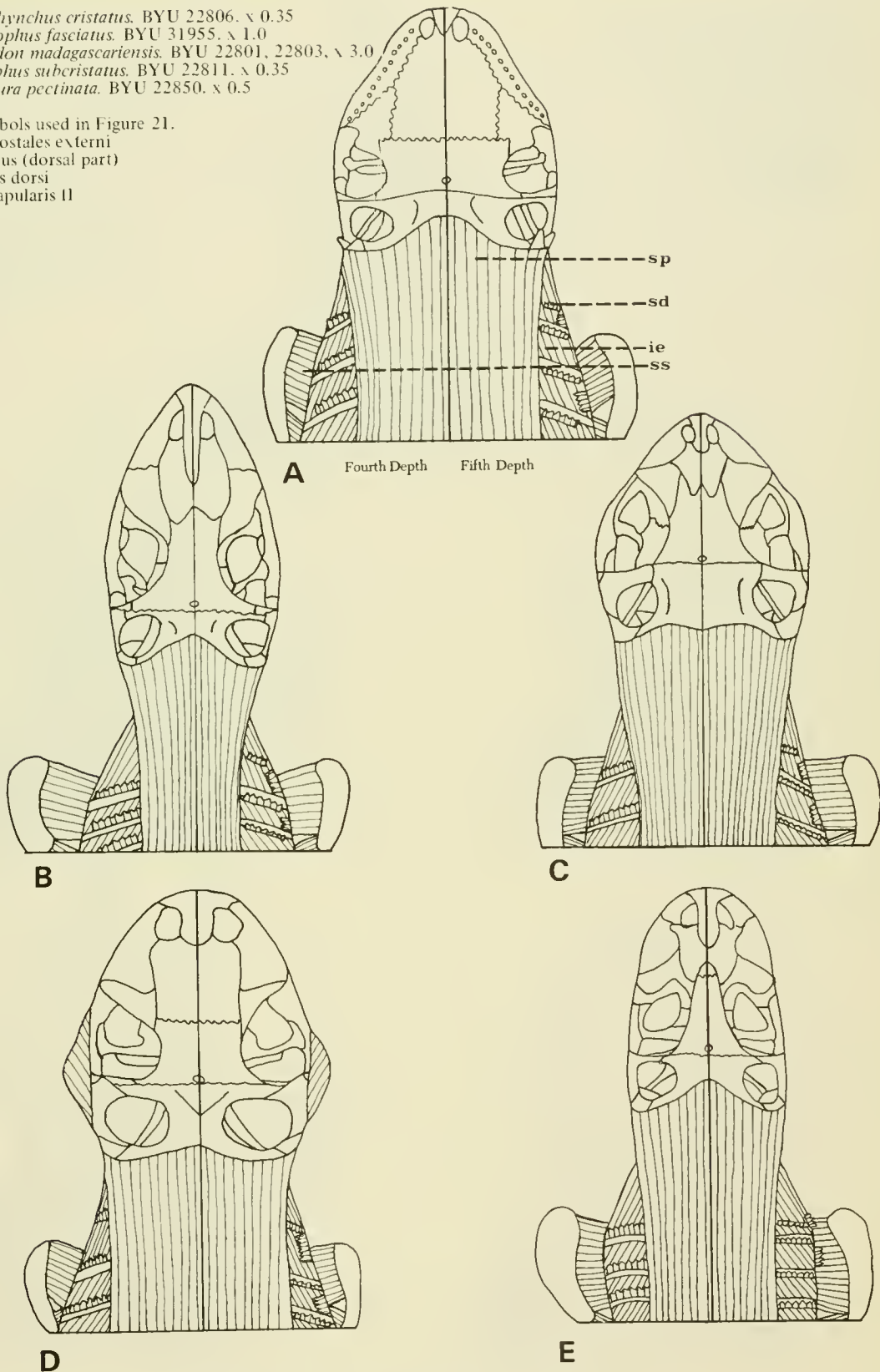


Figure 21. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right.

- A. *Cyclura nuchalis*. BYU 22799. x 1.0
B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
C. *Iguana iguana*. BYU 22851. x 0.75
D. *Oplurus sebae*. BYU 11504. x 1.25
E. *Sauromalus obesus*. BYU 31953. x 1.5

Key to symbols used in Figure 22.
ie-intercostales externi
sd-serratus (dorsal part)
sp-spinus dorsi
ss-subscapularis II

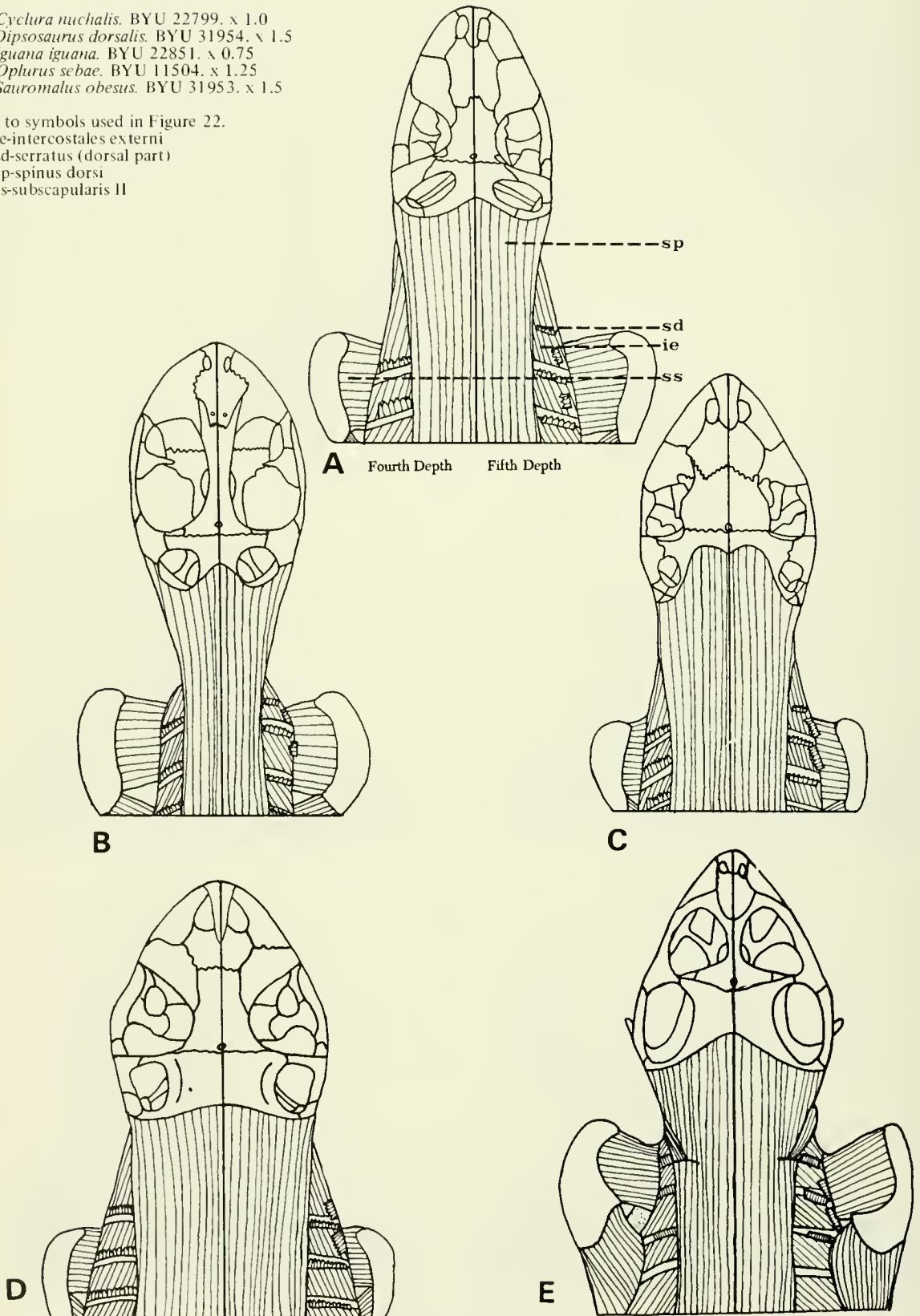


Figure 22. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right.

- A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 0.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 23.
am-adductor mandibularis externus medius
as-adductor mandibularis externus superficialis
au-auditory meatus
cc-constrictor colli
cm-cervicomandibularis
dm-depressor mandibularis
ep-episternocleidomastoideus
ip-intermandibularis posterior
la-levator angularis oris
tr-trapezius

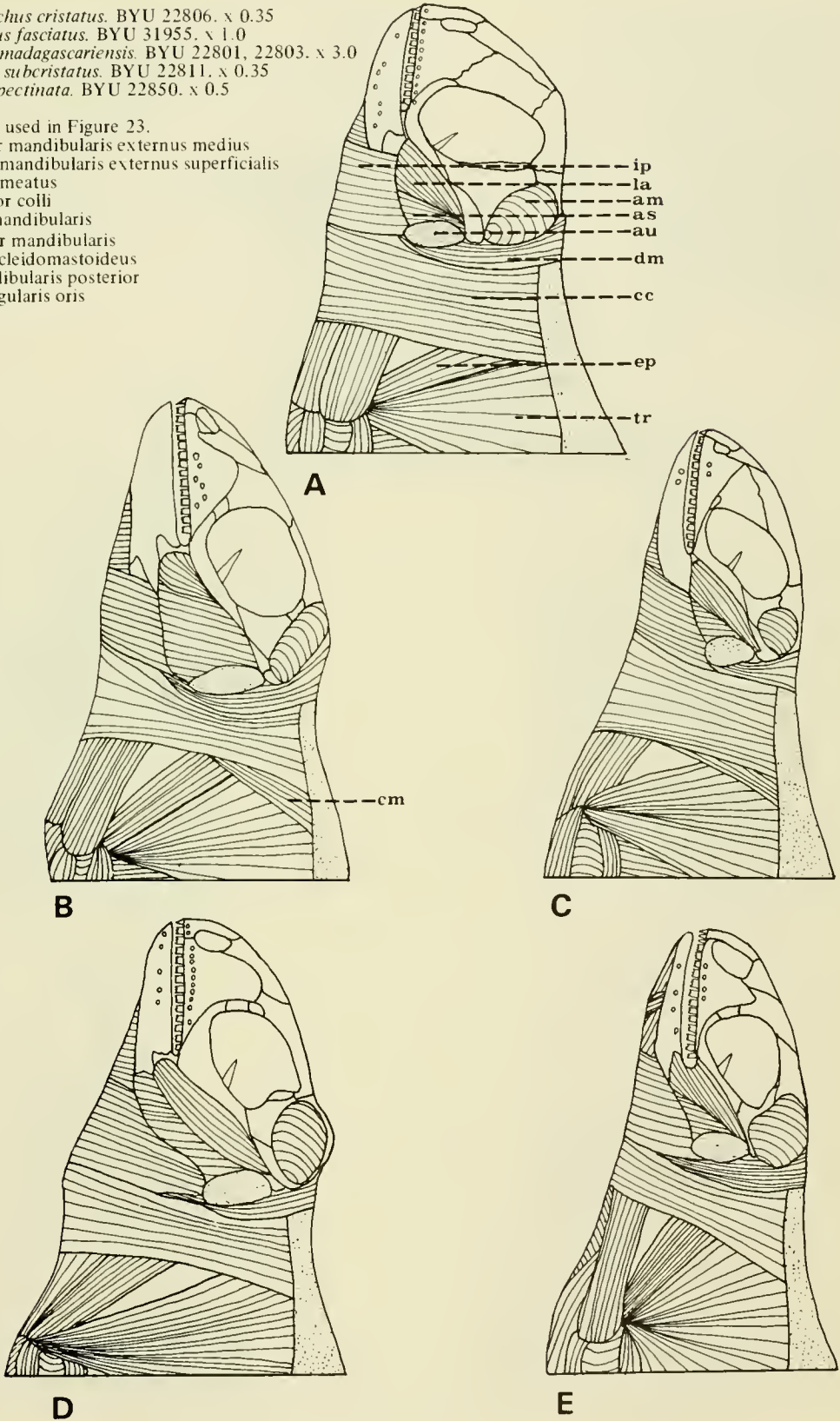


Figure 23. Lateral view of head and neck musculature; superficial depth.

- A. *Cychura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 33851. $\times 0.75$
 D. *Oplurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 24.

am-adductor mandibularis externus medius
 as-adductor mandibularis externus superficialis
 au-auditory meatus
 cc-constrictor colli
 cm-cervicomandibularis
 dm-depressor mandibularis
 ep-episternocleidomastoideus
 ip-intermandibularis posterior
 la-levator angularis oris
 tr-trapezius

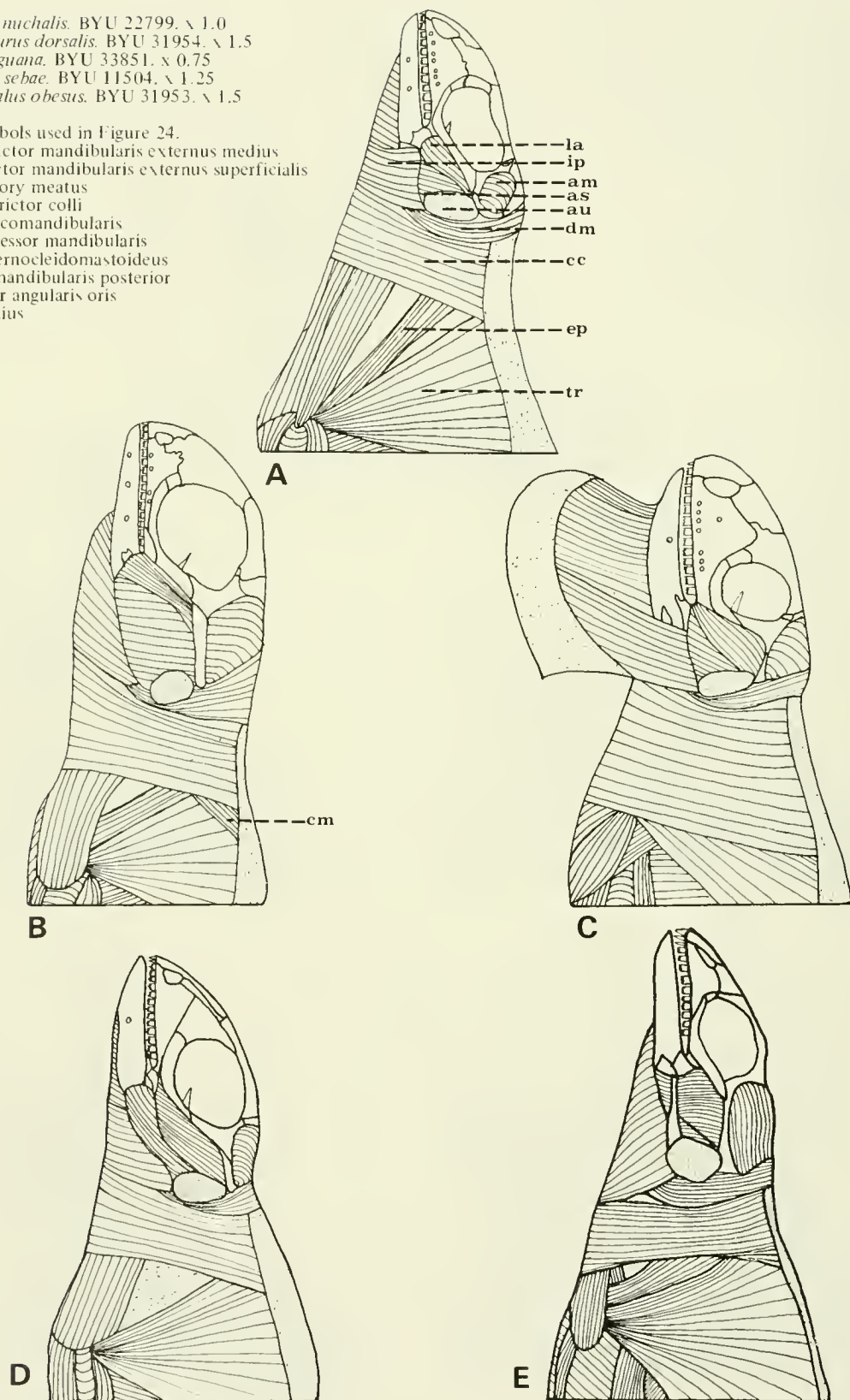


Figure 24. Lateral view of head and neck musculature; superficial depth.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
C. *Chalarodon madagascariensis*. BYU 22801, 22803. $\times 3.0$
D. *Conolophus subcristatus*. BYU 22811. $\times 0.35$
E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 25.

- am-adductor mandibularis externus medius
as-adductor mandibularis externus superficialis
cm-cervicomandibularis
dm-depressor mandibularis
ep-episternocleidomastoideus
ip-intermandibularis posterior
ls-levator scapulae superficialis
om-omohyoideus
sh-sternohyoideus

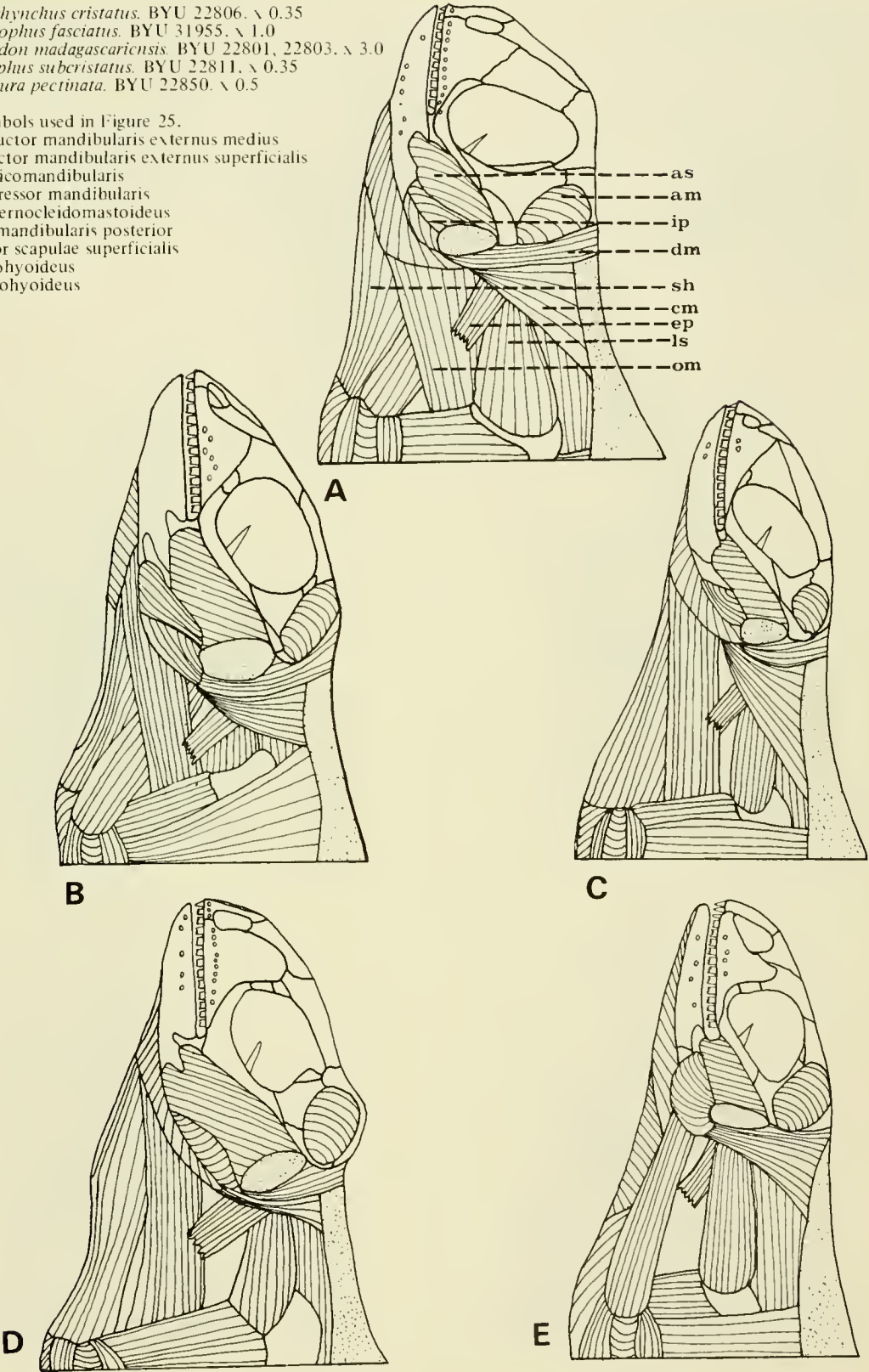


Figure 25. Lateral view of head and neck musculature; first depth.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 22851. $\times 0.75$
 D. *Oplurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 26.

am-adductor mandibularis externus medius
 as-adductor mandibularis externus superficialis
 cm-cervicomandibularis
 dm-depressor mandibularis
 ep-episternocleidomastoideus
 ip-intermandibularis posterior
 ls-levator scapulae superficialis
 om-omohyoideus
 sh-sternohyoideus

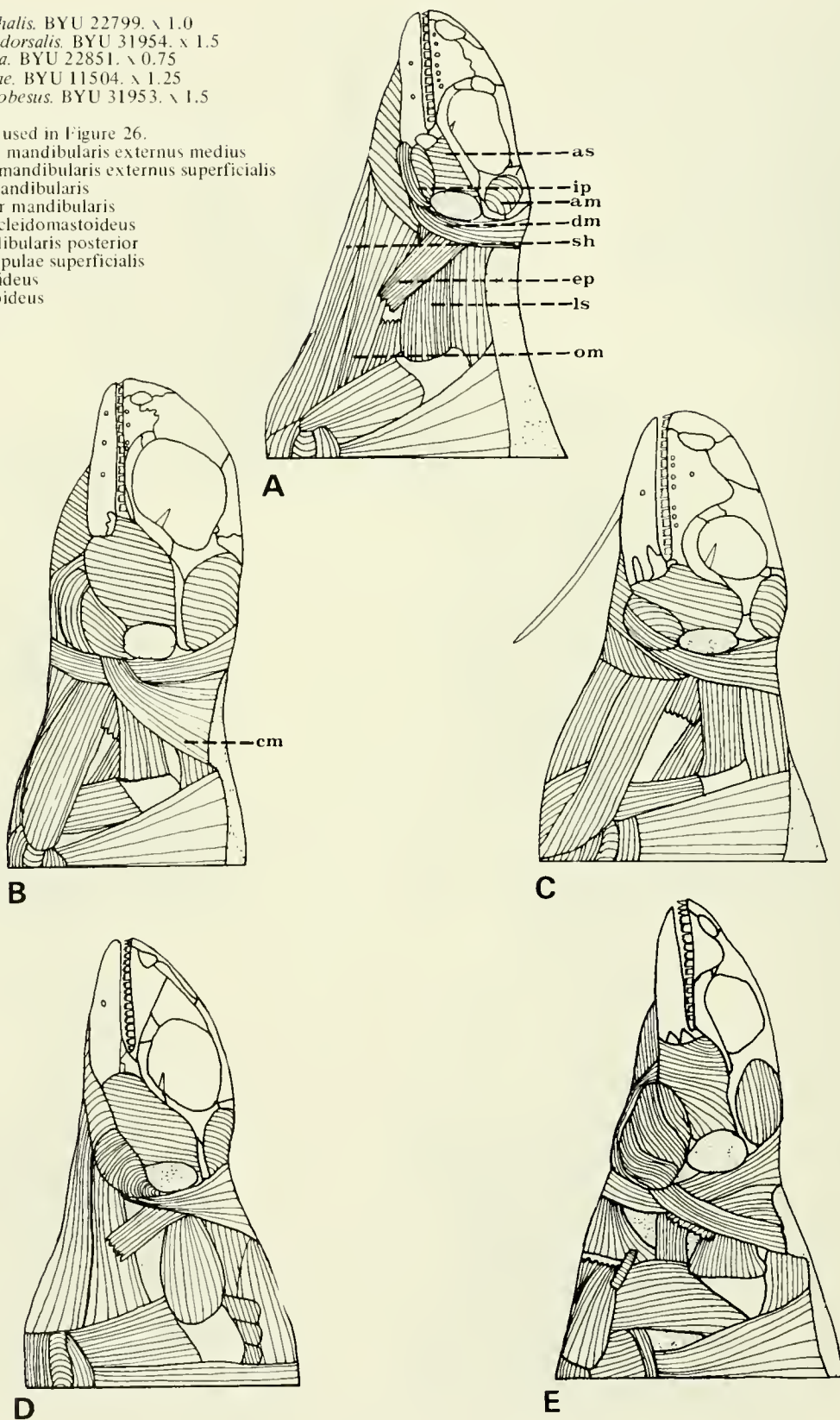


Figure 26. Lateral view of head and neck musculature; first depth.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
C. *Chalarodon madagascariensis*. BYU 22801, 22803. $\times 3.0$
D. *Conolophus suberistatus*. BYU 22811. $\times 0.35$
E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 27.
am-adductor mandibularis externus medius
ep-episternocleidomastoideus
lp-levator scapulae profundus
ls-levator scapulae superficialis
pm-pharyngeal membrane

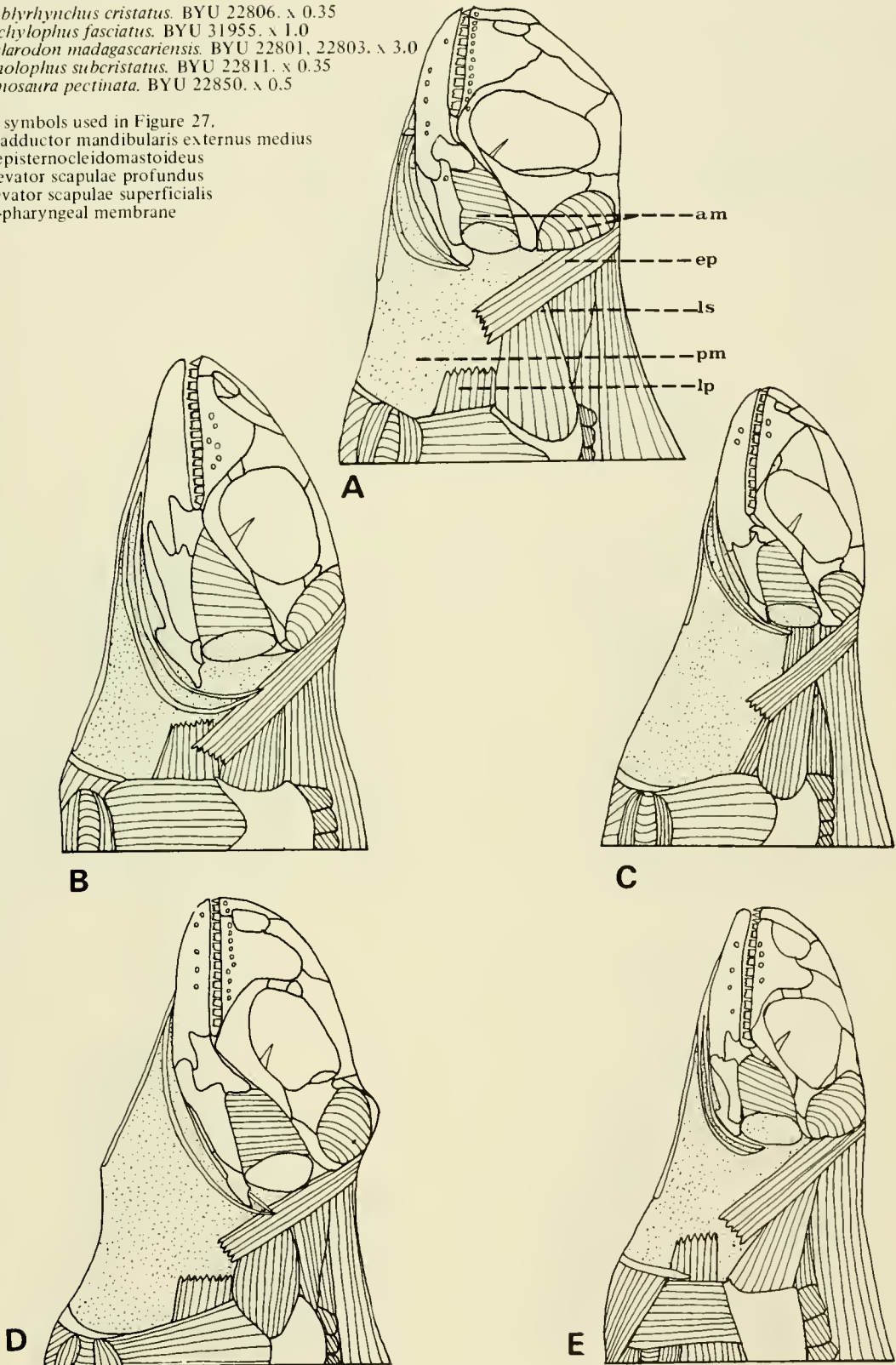


Figure 27. Lateral view of head and neck musculature;
second depth.

- A. *Cyclura nuchalis*. BYU 22799. x 1.0
- B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
- C. *Iguana iguana*. BYU 22851. x 0.75
- D. *Oplurus sebae*. BYU 11504. x 1.25
- E. *Sauromalus obesus*. BYU 31953. x 1.5

Key to symbols used in Figure 28.
am-adductor mandibularis externus medius
ep-episternocleidomastoideus
lp-levator scapulae profundus
ls-levator scapulae superficialis
pm-pharyngeal membrane

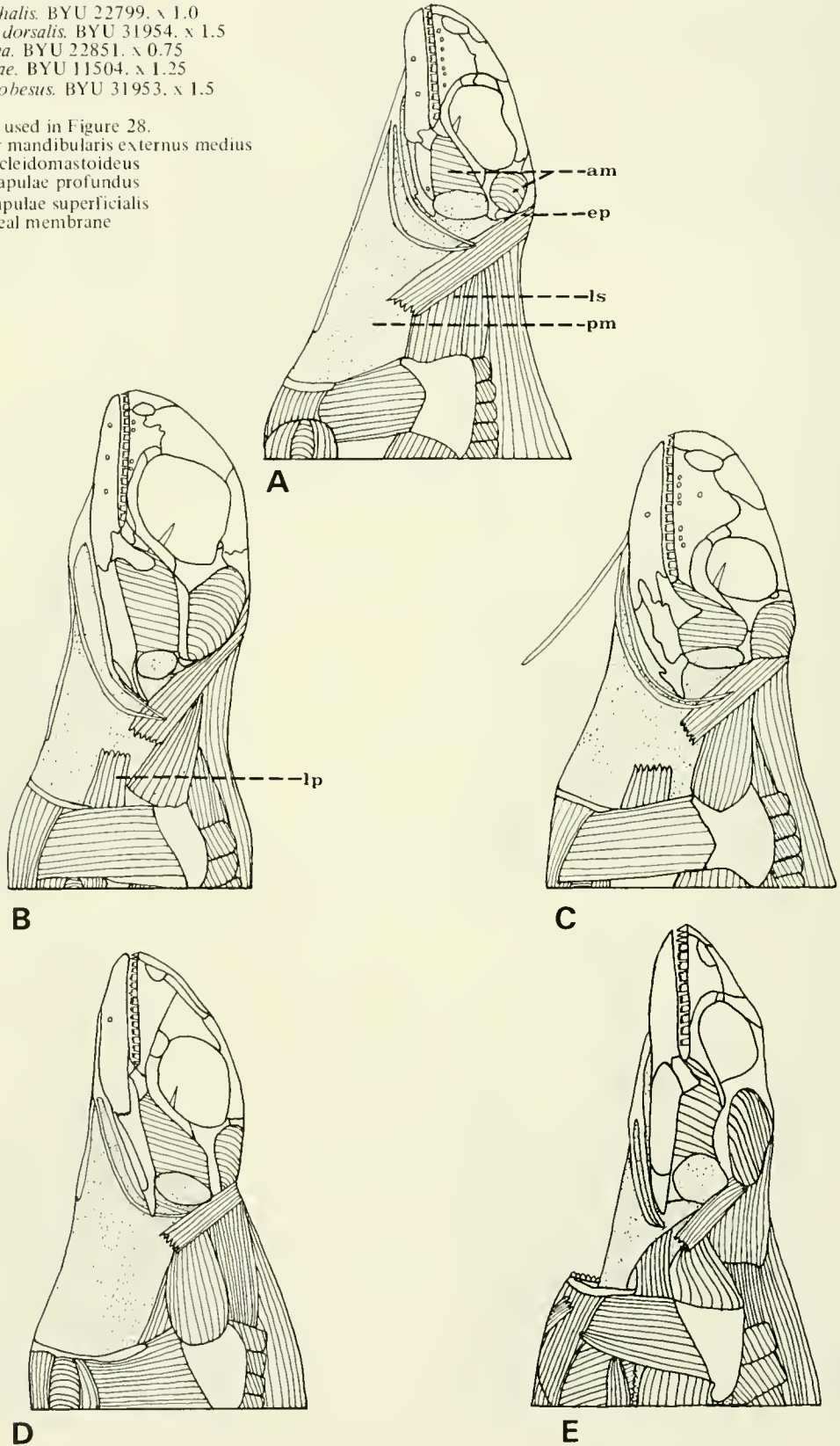


Figure 28. Lateral view of head and neck musculature;
second depth.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 0.35$
- B. *Brachylophus fasciatus*. BYU 31955. $\times 1.0$
- C. *Chalarondon madagascariensis*. BYU 22801, 22803. $\times 3.0$
- D. *Conolophus suberistatus*. BYU 22811. $\times 0.35$
- E. *Ctenosaura pectinata*. BYU 22850. $\times 0.5$

Key to symbols used in Figure 29.
ap-adductor mandibularis externus profundus
lp-levator scapulae profundus
ls-levator scapulae superficialis
ps-pseudotemporalis superficialis

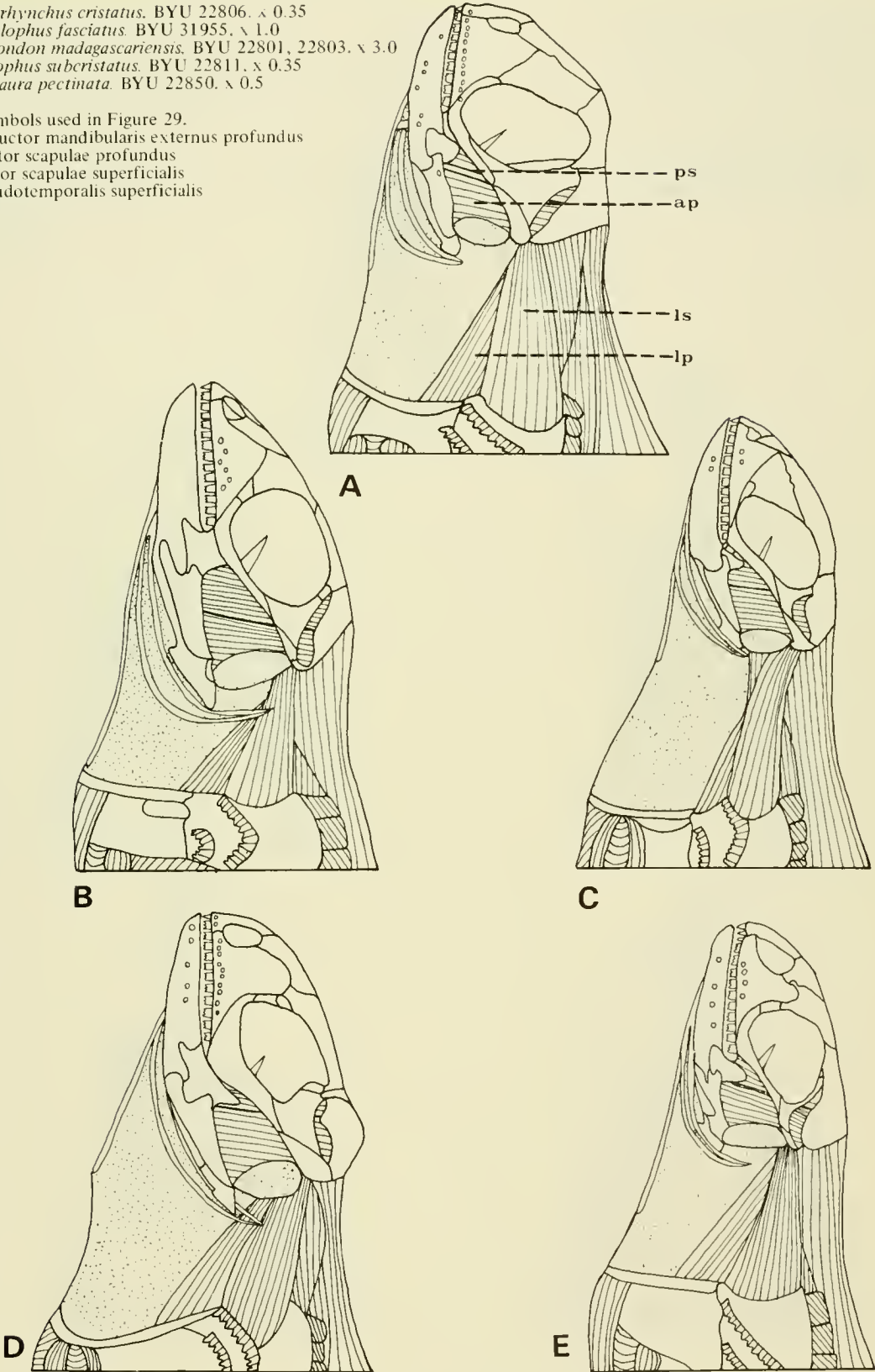


Figure 29. Lateral view of head and neck musculature; third depth.

- A. *Cyclura nuchalis*. BYU 22799. x 1.0
- B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
- C. *Iguana iguana*. BYU 22851. x 0.75
- D. *Oplurus sebae*. BYU 11504. x 1.25
- E. *Sauromalus obesus*. BYU 31953. x 1.5

Key to symbols used in Figure 30.
ap-adductor mandibularis externus profundus
lp-levator scapulae profundus
ls-levator scapulae superficialis
ps-pseudotemporalis superficialis

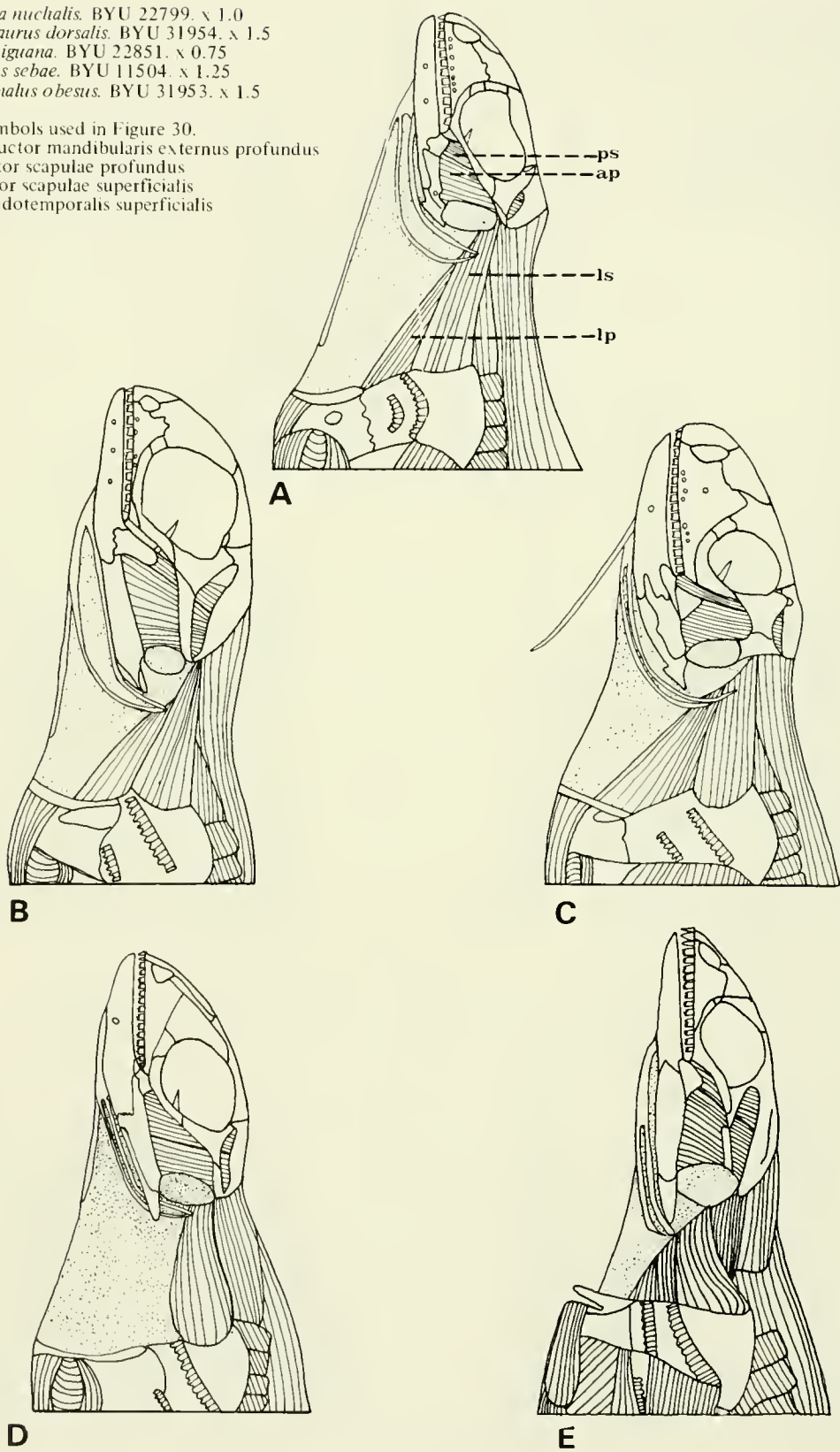


Figure 30. Lateral view of head and neck musculature; third depth.

- A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 0.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 31.
am-adductor mandibularis posterior
lp-levator pterygoideus
pp-protractor pterygoideus
pt-pseudotemporalis profundus
sc-scapula
sd-spinus dorsi
ss-suprascapula

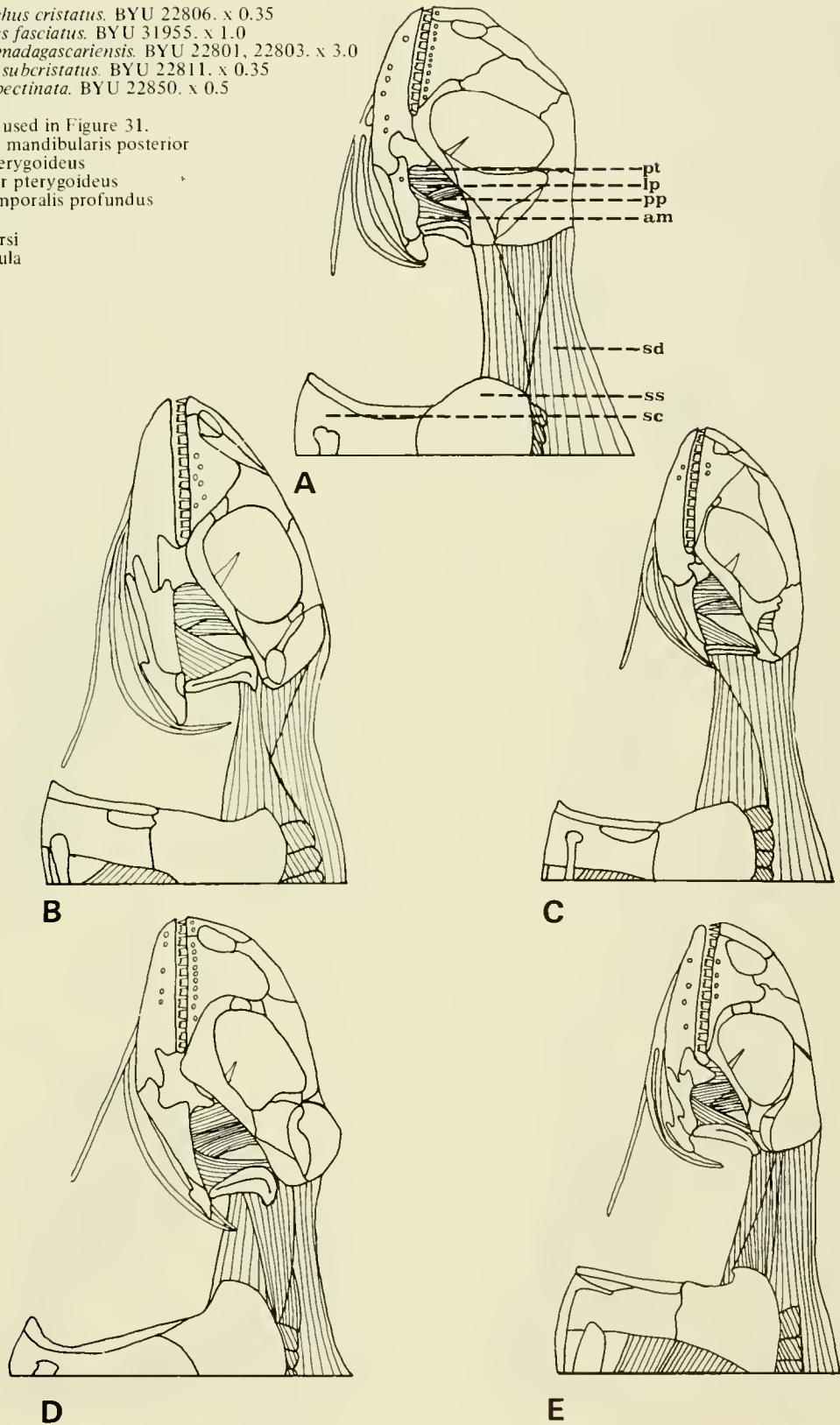


Figure 31. Lateral view of head and neck musculature; fourth depth.

- A. *Cyclura nuchalis*. BYU 22799. $\times 1.0$
 B. *Dipsosaurus dorsalis*. BYU 31954. $\times 1.5$
 C. *Iguana iguana*. BYU 22851. $\times 1.25$
 D. *Ophurus sebae*. BYU 11504. $\times 1.25$
 E. *Sauromalus obesus*. BYU 31953. $\times 1.5$

Key to symbols used in Figure 32.

am-adductor mandibularis posterior
 lp-levator pterygoideus
 pp-protractor pterygoideus
 pt-protractor pterygoideus
 pt-pseudotemporalis profundus
 se-scapula
 sd-spinus dorsi
 ss-suprascapula

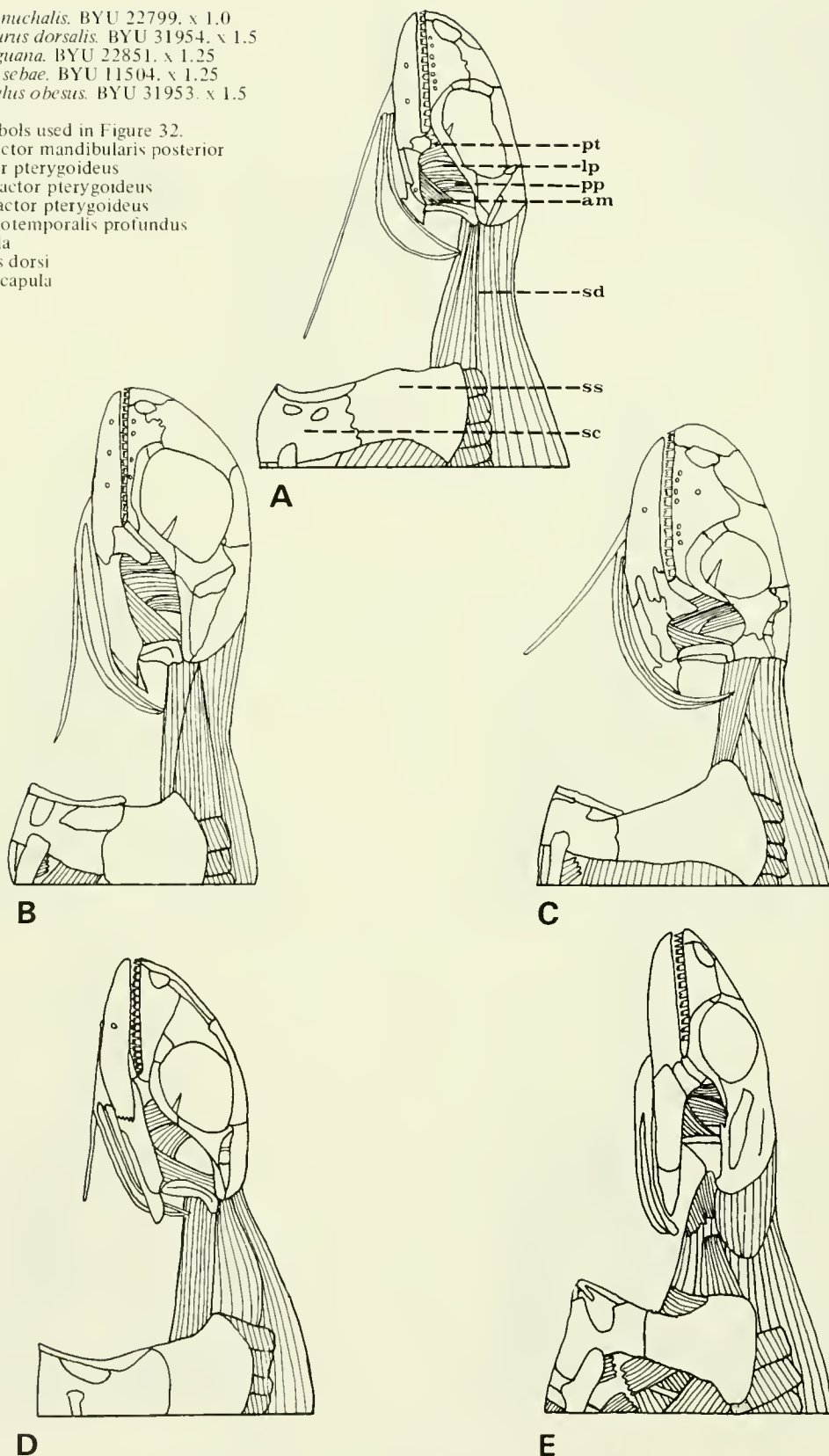


Figure 32. Lateral view of head and neck musculature; fourth depth.

- A. *Amblyrhynchus cristatus*. BYU 22806. x 0.35
B. *Brachylophus fasciatus*. BYU 31955. x 1.0
C. *Chalarodon madagascariensis*. BYU 22801, 22803. x 3.0
D. *Conolophus subcristatus*. BYU 22811. x 0.35
E. *Ctenosaura pectinata*. BYU 22850. x 0.5

Key to symbols used in Figure 33.

- cl-clavicle
ic-interclavicle
lp-levator pterygoideus
pp-protractor pterygoideus
sd-spinus dorsi
se-serratus (dorsal part)
sl-sacrolumbalis

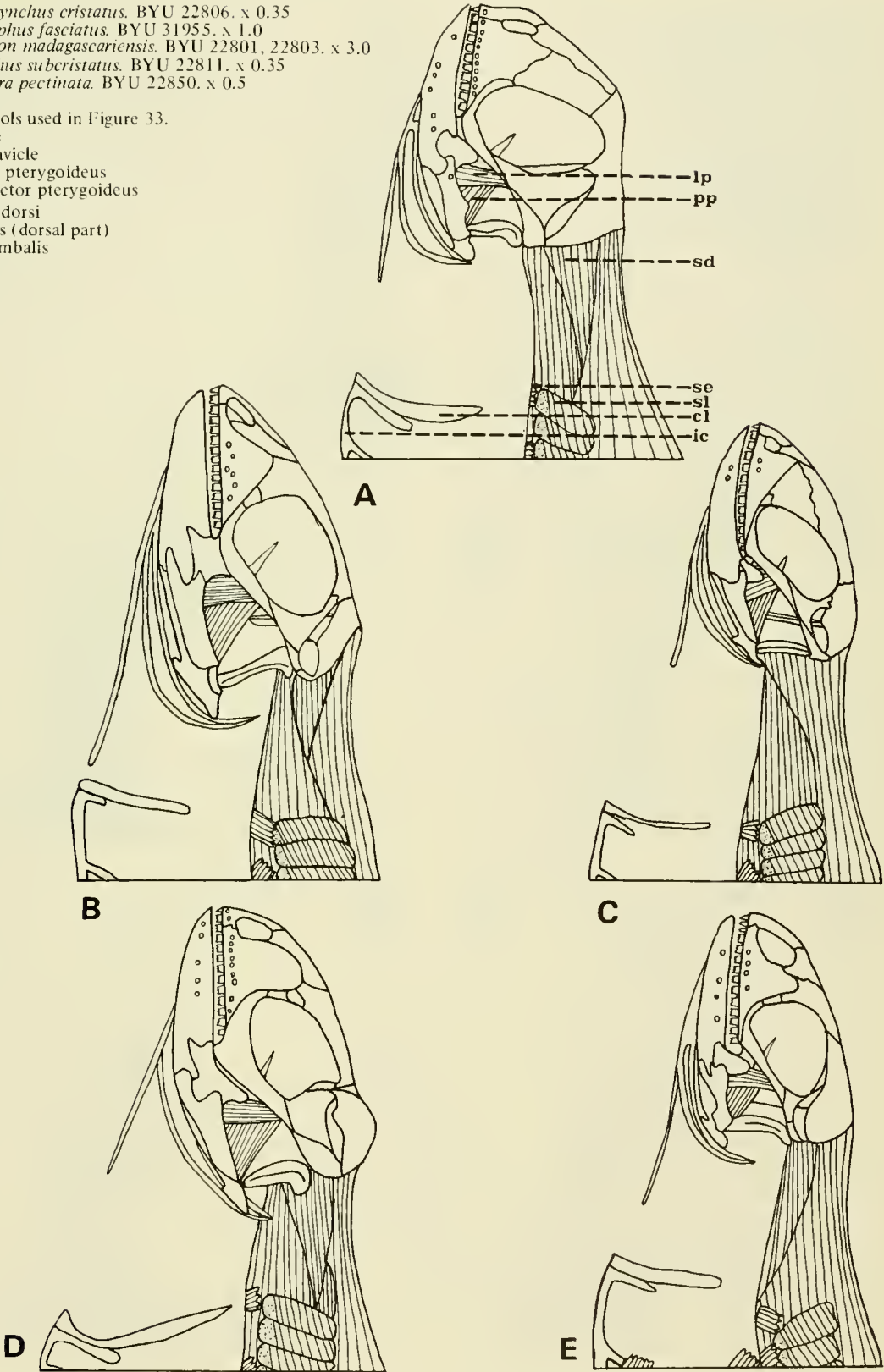


Figure 33. Lateral view of head and neck musculature; fifth depth.

- A. *Cyclura nuchalis*. BYU 22799. x 1.0
 B. *Dipsosaurus dorsalis*. BYU 31954. x 1.5
 C. *Iguana iguana*. BYU 22851. x 1.25
 D. *Ophurus sebae*. BYU 11504. x 1.25
 E. *Sauromalus obesus*. BYU 31953. x 1.5

Key to symbols used in Figure 34.

cl-clavicle
 ic-interclavicle
 lp-levator pterygoideus
 pp-protractor pterygoideus
 sd-spinus dorsi
 se-serratus (dorsal part)
 sl-sacrolumbalis

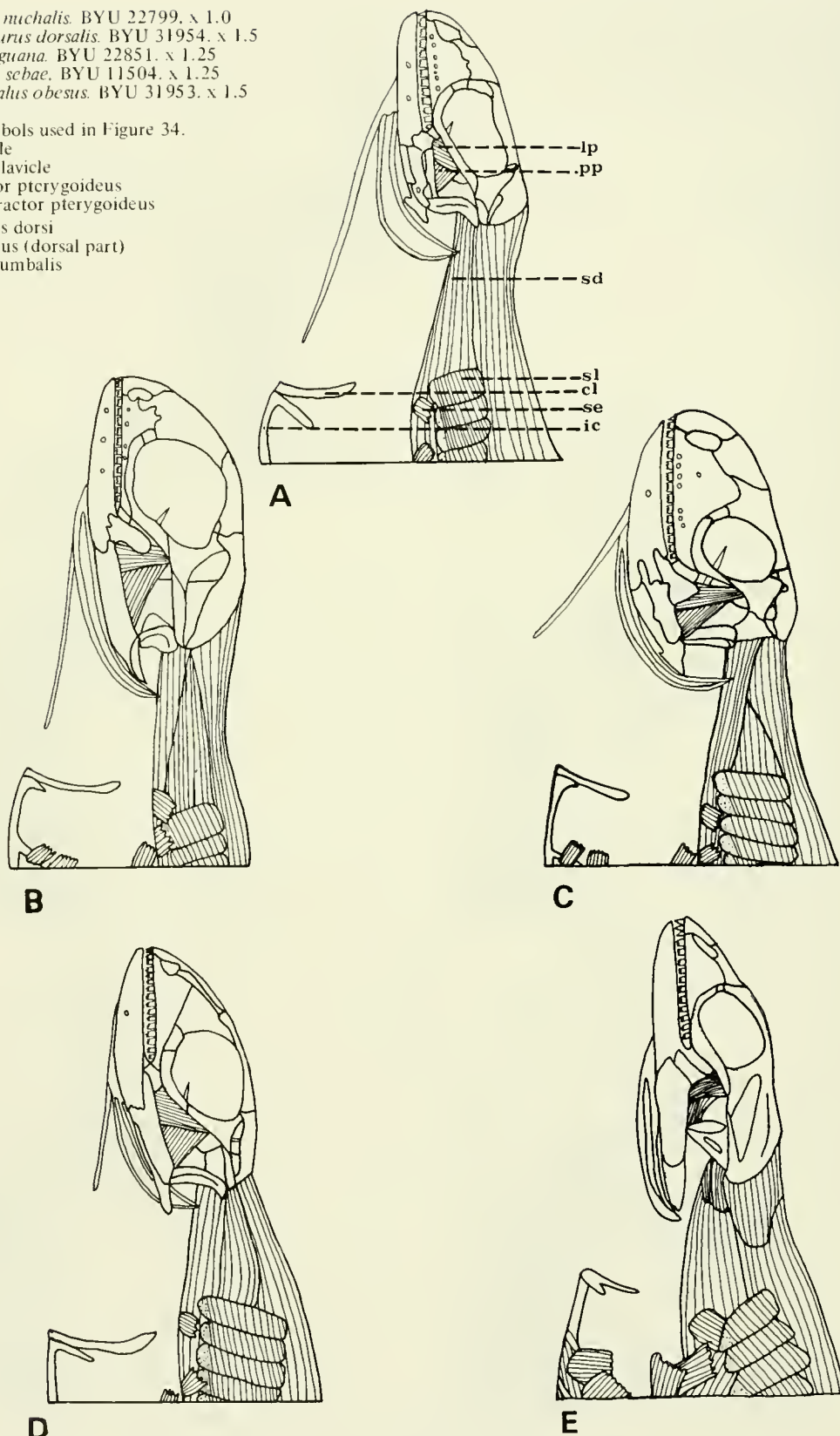


Figure 34. Lateral view of head and neck musculature; fifth depth.

- A. *Amblyrhynchus cristatus*. BYU 22810. x 1.25
B. *Brachylophus fasciatus*. BYU 23743. x 1.5
C. *Chalarodon madagascariensis*. BYU 22801. x 6.0
D. *Conolophus subcristatus*. BYU 22811. x 1.0
E. *Ctenosaura pectinata*. BYU 22796. x 1.5
F. *Cyclura nuchalis*. BYU 22799. x 2.5
G. *Dipsosaurus dorsalis*. BYU 23761. x 3.0
H. *Iguana iguana*. BYU 22852. x 1.25
I. *Ophurus sebae*. BYU 11504. x 2.5
J. *Sauromalus obesus*. BYU 23762. x 1.5

Key to symbols used in Figure 35.

- ac-anterior cleft
fp-filamentous papillae
gl-glottis
pc-posterior cleft
pp-pointed papillae

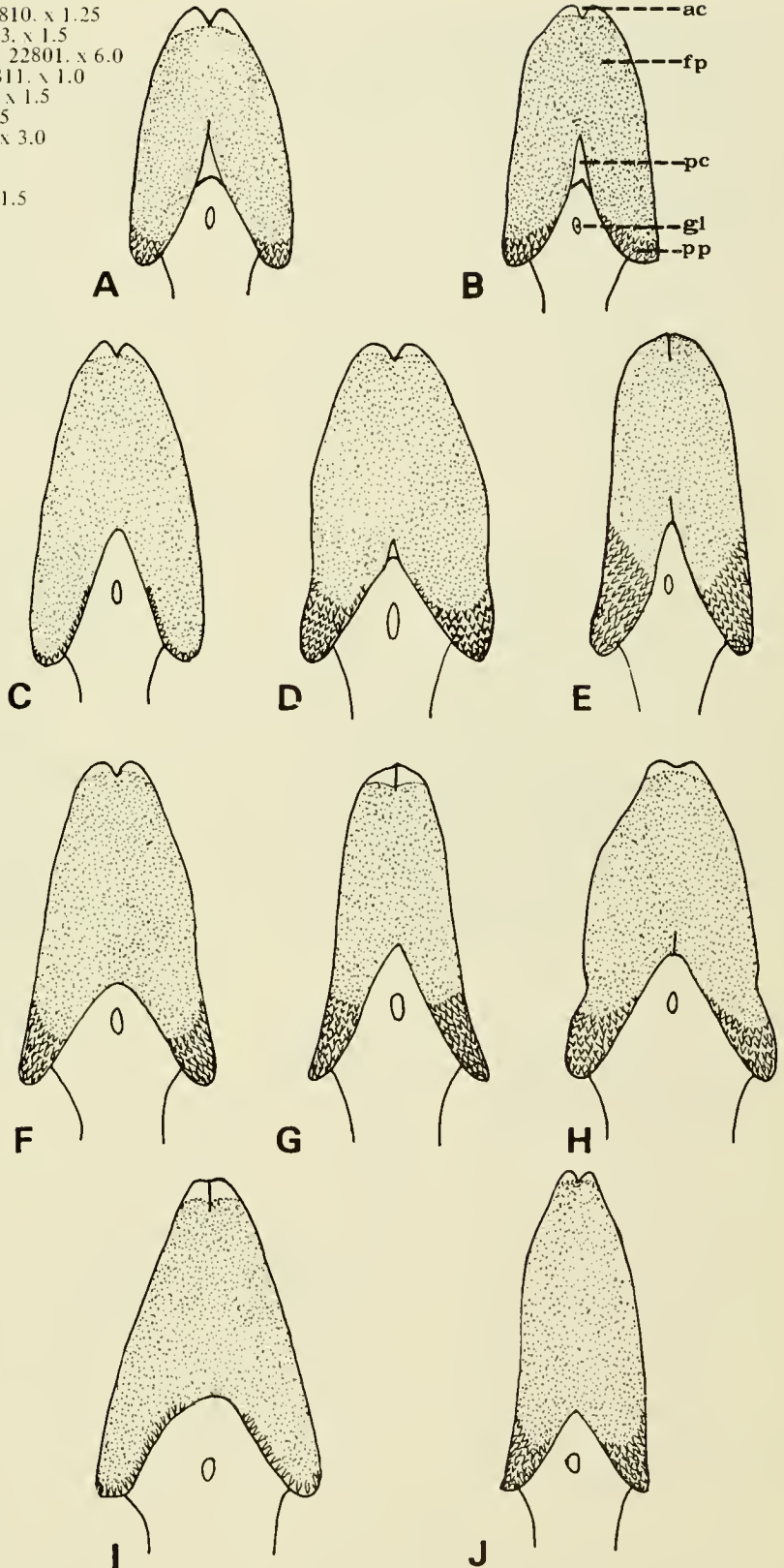


Figure 35. Dorsal view of the tongue.

- A. *Amblyrhynchus cristatus*. BYU 22806. $\times 1.5$. Left hemipenis.
 B. *Brachylophus fasciatus*. BYU 23743. $\times 2.0$. Left hemipenis.
 C. *Ctenosaura pectinata*. BYU 22796. $\times 2.0$. Left hemipenis.
 D. *Dipsosaurus dorsalis*. BYU 23760. $\times 4.0$. Left hemipenis.
 E. *Iguana iguana*. BYU 22851. $\times 2.0$. Left hemipenis.
 F. *Sauromalus obesus*. BYU 23762. $\times 3.0$. Right hemipenis.

Key to symbols used in Figure 36.

cr-crease

cs-calyculate surface

ss-sulcus spermaticus

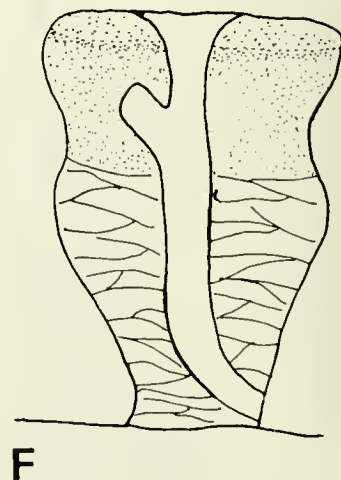
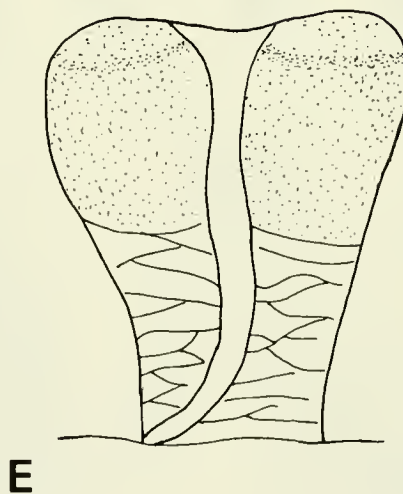
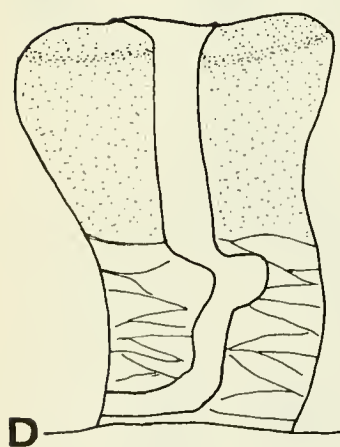
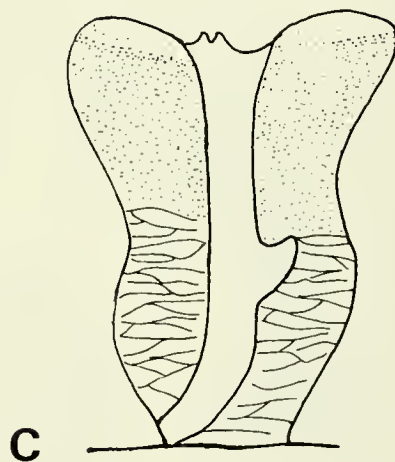
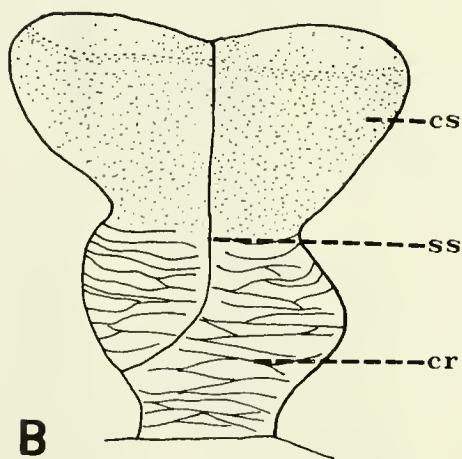
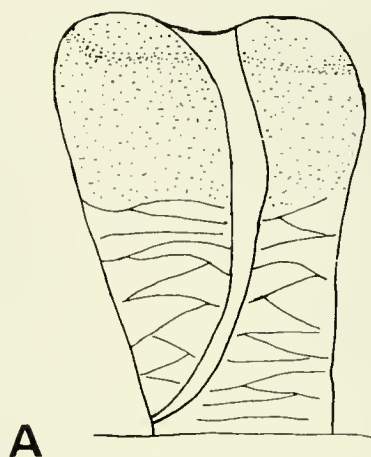


Figure 36. Hemipenes

Hemipenes

The vocabulary for descriptions of the hemipenes will follow that of Cope (1896) and Dowling and Savage (1960). Only the hemipenes (Figure 36) of *Amblyrhynchus*, *Brachylophus*, *Ctenosaura*, *Dipsosaurus*, *Iguana*, and *Sauromalus* were available for study.

Cope (1896) found the hemipenes to be undivided in *Cyclura* and *Iguana*, and bilobate in *Ctenosaura*, *Dipsosaurus*, and *Sauromalus*. He also noted calyces covering the distal ends of all the above genera.

In our investigations, we have found the hemipenes of all the genera to be bulbous rather than bilo-

bate in *Sauromalus*, *Dipsosaurus*, *Amblyrhynchus*, and *Iguana*. *Ctenosaura* and *Brachylophus* are more bilobate than the above genera. However, *Brachylophus* has the most bilobate hemipenes of the group.

The sulcus spermaticus forms a broad, open curving groove on the posterior surface of the hemipenis in all genera except *Brachylophus*, where the sulcus is narrow and tightly closed forming a tube rather than a groove. In *Ctenosaura*, *Sauromalus* and *Dipsosaurus*, a fold exists on the lateral border of the sulcus forming a small diverticulum in that area.

The distal half of the hemipenis is calyculate on the surface, whereas the base and proximal half is covered with irregular creases in all genera. All hemipenes lack spines or spinose structures.

DISCUSSION

The phylogenetic relationships between the genera of iguanine lizards have not been analyzed. Boulenger (1890) outlined some osteological characteristics for most of the genera but made no attempt at defining relationships. Cope, in 1892, discussed *Dipsosaurus* and indicated it to be related to *Crotaphytus* by general appearance but different from it osteologically. Cope also analyzed *Sauromalus* and by virtue of the zygosphenal articulation, allied "... it to *Dipsosaurus* and the larger Iguanidae, but the separated ceratobranchials, and wide sternum are like that of the Phrynosomas, with the exception of the fontanelles" (Cope, 1892:205). Camp (1923) in his basic work on the classification of lizards indicated *Iguana*, *Cyclura*, *Sauromalus*, *Dipsosaurus*, and *Amblyrhynchus* to be related and intermediate in primitiveness. He also allied *Brachylophus* to *Ctenosaura* and *Cyclura* "... on the basis of details of the throat musculature, and number of abdominal parasterna" (Camp, 1923:416).

In 1942 Mittleman considered the relationships between *Uta*, *Urosaurus* and the iguanines *Sauromalus*, *Dipsosaurus*, and *Ctenosaura*. He indicated that these latter three herbivores were a primitive ancestral stock closely related to *Sceloporus* and *Crotaphytus*. Savage (1958) outlined the iguanine characteristics and included *Crotaphytus* in that evolutionary line. Avery and Tanner (1964) were able to show several myological differences between *Sauromalus* and *Crotaphytus* and indicated these two genera were not in the same evolutionary line. Etheridge, in 1964, also examined the iguanines and separated the genus *Crotaphytus* from them, based on osteological differences.

As a result of previous studies, the existence of an iguanine evolutionary line has been well established. However, no conclusions have been made concerning the relationships between genera and the general phylogeny of the iguanine line.

Osteology

As previously indicated, length-width measurements of bones and bone shapes were utilized to analyze the osteological relationships between the iguanines. The ratio means of tables 1-34 were used to make these relationships clear. It has been assumed that a difference of forty or less points between means of the same bone indicates a close relationship. The possession of bones with similar shape is also an indicator of close relationship. Those genera sharing the most characters in common are considered to be the most closely related. A summary of the number of characters shared between genera is found in table 37.

TABLE 37
THE NUMBER OF OSTEOLOGICAL SIMILARITIES BETWEEN GENERA

Genus	<i>Amblyrhynchus</i>	<i>Brachylophus</i>	<i>Chalarodon</i>	<i>Conolophus</i>	<i>Ctenosaura</i>	<i>Cyclura</i>	<i>Dipsosaurus</i>	<i>Enyalosaurus</i>	<i>Iguana</i>	<i>Oplurus</i>	<i>Sauromalus</i>
<i>Amblyrhynchus</i>	x	12	8	22	8	10	13	11	17	10	13
<i>Brachylophus</i>	12	x	14	19	21	24	27	10	22	17	21
<i>Chalarodon</i>	8	14	x	11	15	10	13	13	11	24	10
<i>Conolophus</i>	22	19	11	x	22	22	20	11	22	14	12
<i>Ctenosaura</i>	8	21	15	22	x	31	17	23	32	19	27
<i>Cyclura</i>	10	24	10	22	31	x	16	17	28	18	26
<i>Dipsosaurus</i>	13	27	13	20	17	16	x	9	17	15	15
<i>Enyalosaurus</i>	11	10	13	11	23	17	9	x	13	12	16
<i>Iguana</i>	17	22	11	22	32	28	17	13	x	15	24
<i>Oplurus</i>	10	17	24	14	19	18	15	12	15	x	16
<i>Sauromalus</i>	13	21	10	12	27	26	15	16	24	16	x

Etheridge (1965:166) commented on the uniqueness of the abdominal skeleton of *Chalarodon* and *Oplurus*. These genera, by virtue of their abdominal skeleton, are either more primitive than, or as primi-

tive as, any member of the iguane line. Because these two genera are isolated on Madagascar, one would assume that they are closely related. *Oplurus* and *Chalarodon* share 24 characters in common. This degree of relationship is higher than that of *Oplurus* or *Chalarodon* with any other genus. *Oplurus* also shares a number of close relationships with other genera. There are 19 characters shared in common between *Oplurus* and *Ctenosaura*, 18 between *Oplurus* and *Cyclura*, and 17 between *Oplurus* and *Brachylophus*. On the other hand, *Chalarodon* shows no close relationships with other genera except *Oplurus*. The only other high number of shared characters is that of *Chalarodon* with *Ctenosaura* (15).

It is obvious from the above that *Oplurus* is more closely related to the iguanines than *Chalarodon*. *Chalarodon* shows so few characters in common with the iguanines that we do not consider it to be closely related to the iguane line of evolution. The high number of characters shared in common between *Chalarodon* and *Oplurus* is probably the result of a distant common ancestry between the two genera and common adaptations needed to meet the environmental demands of Madagascar.

Based on anatomy, we consider *Oplurus*, although primitive, to be more closely related to the iguanines than *Chalarodon*. Both are primitive, have been isolated for a long time, and have radiated. We consider the Madagascar iguanids to be the most primitive members of the family.

In regards to the iguane line, the primitive iguanid *Oplurus* is more closely related to *Ctenosaura*, with 19 characters shared, and *Cyclura*, with 18 shared characters. This suggests that *Ctenosaura* is the most primitive of the Western Hemisphere iguanines. The primitiveness of *Ctenosaura* has been previously suggested by Mittleman (1942:113) who placed it as ancestral to all North American Iguanidae. This form may not be ancestral to all North American iguanids but is certainly ancestral to the Western Hemisphere iguanines. Besides possessing more characters in common with *Oplurus* than any other iguane, *Ctenosaura* also shares characters in common with *Conolophus* (22), *Cyclura* (31), *Iguana* (32) and *Sauromalus* (27). If *Ctenosaura* is not primitive, it is at least in the center of the evolution of the terrestrial Western Hemisphere iguanines.

Cyclura is very close to *Ctenosaura* in structure and in the number of osteological characters shared (31). *Cyclura* is also closely related to *Iguana* with which it shares 28 characters. *Cyclura* is an island form, probably evolved from the *Ctenosaura* line by isolation.

Iguana appears to have much in common with both *Cyclura* (28 characters shared) and *Ctenosaura* (32 characters shared). Together *Ctenosaura*, *Iguana*, and *Cyclura* form a closely related natural group and probably represent a primary radiation in the Central

American area of the Western Hemisphere.

Sauromalus is a northern extension of the *Ctenosaura* type. *Sauromalus* shows 27 characters in common with *Ctenosaura* while 26 characters are shared with *Cyclura* and 24 with *Iguana*. It is logical to assume that *Sauromalus*, a desert form, has evolved from a *Ctenosaura* type organism, a more tropical form, rather than a *Cyclura* type. *Ctenosaura* and *Sauromalus* are both continental rather than island forms, such as *Cyclura*, and *Ctenosaura* and *Sauromalus* overlap ranges in Mexico and Baja, California.

Conolophus shares 22 characters each with *Amblyrhynchus*, *Ctenosaura*, *Cyclura*, and *Iguana*. This is an indication that this representative of the Galapagos Island fauna is derived from the Central American radiation rather than elsewhere.

After eliminating all characters shared in common between all five genera, one finds more are shared with *Ctenosaura* than *Cyclura*, *Iguana*, and *Amblyrhynchus*. The size of the interclavicle arms, the placement of the anterior inferior alveolar foramen in the splenial bone, the size and shape of the lacrimal bone, size and shape of the postfrontal, size and shape of the angular process in the lower jaw, size of the supraoccipital, size of the fenestra exonarina, size and shape of the angular bone, and size of the supratemporal fossa all link *Conolophus* with *Ctenosaura* rather than with either of the other three genera.

Amblyrhynchus is closely related to *Conolophus* with 22 characters shared, and to *Iguana* with 17 characters shared. An analysis of these shared characters shows that *Amblyrhynchus* is more closely related to *Conolophus* than to *Iguana*. After eliminating the characters shared in common by all three genera one finds that *Amblyrhynchus* shares 12 characters with *Conolophus* as opposed to 6 for *Iguana*. Among the characters shared in common with *Conolophus* are the size of the supraoccipital, palatine, jugal, quadrate, supratemporal fossa, fenestra exonarina, dentary and size of angular process. Also the posterior border of the dentary forms a complex inter-fingering suture with the surangular bone. The frontal bone in both is wider than long, and the pyriform recess widens posteriorly at a sharp angle in both genera. *Amblyrhynchus* shares with *Iguana* the size of the lacrimal bones, parietal wings, and the orbit. The angular process has a similar shape in both genera and the interclavicles are the same shape with arms equal in length to the body and attached to the body at a 90° angle. *Conolophus* and *Amblyrhynchus* are more closely related to each other than to other iguanines. *Amblyrhynchus* is probably derived from a *Conolophus-Ctenosaura* ancestor which invaded the Galapagos Islands from the mainland.

Brachylophus, from Fiji and Tonga Islands, is the most geographically isolated iguane. This genus shares a large number of characters with *Cyclura* (24), *Iguana* (22), *Ctenosaura* (21), and *Sauromalus* (21).

Obviously this close relationship to all these genera indicates a point of origin some place in the primary Central American radiation. *Sauromalus* being a Northern representative of this group is the least likely relative of *Brachylophus*. When all common characters between the five genera are eliminated we find the three characters, the size of the postfrontals, prefrontals and articular bones are shared between *Brachylophus* and *Cyclura*. *Brachylophus* and *Ctenosaura* share nasals, parietal wings, orbits, and articulars of similar size and shape. *Iguana* and *Brachylophus* have similar palatines, premaxillas, quadrates and vomers. *Brachylophus*, as with *Conolophus*, with which it shares 19 characters, is probably evolved from the pre-*Ctenosaura-Iguana* ancestral stock.

Dipsosaurus is the most problematical genus in the iguanine line. Osteologically, as pointed out by Cope (1892:201), *Dipsosaurus* is different from the other Iguanidae. This genus differs from all other iguanines in lacking pterygoid teeth, having a convex dentary suture with the surangular, interclavicle arms that attach to the inter-clavicle body at a 30° angle, and an anterior inferior alveolar foramen found in the dentary instead of the splenial bone. A summary of the characters shared with other genera shows that *Dipsosaurus* shares more characters in common with *Brachylophus* (27), than with any other genus. No other genus is even close in its relationship to *Dipsosaurus*. The size ratios of the frontals, parietals, jugals, nasals, squamosals, quadrates, postorbitals, orbits, dentaries, surangulars, splenials, articulars, angulars, angular processes are similar. Also the interclavicle arms are one quarter the length of the interclavicle body, the sternal cartilage possess one fontanelle, the angular process is triangular, and the squamosals are splintlike in both genera. It seems obvious that *Dipso-*

saurus and *Brachylophus* were derived from a common ancestry.

In summary, the osteological characters of the iguanine lizards indicate that *Oplurus* and *Chalarodon* are more closely related to each other than to the iguanines, and *Oplurus* is the Madagascanian genus most closely related to the Western Hemisphere iguanines. Of the iguanines, *Ctenosaura* represents the ancestral stock from which *Cyclura*, *Iguana*, and *Sauromalus* were evolved. *Conolophus* and *Brachylophus* are both early derivatives of this stock as well, with *Amblyrhynchus* having been derived from the *Conolophus* line, and *Dipsosaurus* and *Brachylophus* having a common ancestry.

Before leaving the osteology it is necessary to make mention of *Enyaliosaurus*. Measurements taken on the two skulls examined (USNM 48965 and USNM 21452) show a very close relationship between *Enyaliosaurus* and *Ctenosaura*. The ratio means of over half the skull characters checked confirm this relationship as indicated in table 37. Duellman (1965:599) examined the external morphology of *Enyaliosaurus* and states, "*Enyaliosaurus* doubtless is a derivative of *Ctenosaura*, all species of which are larger and have relatively longer tails with less well-developed spines than *Enyaliosaurus*. The evolutionary trend in *Enyaliosaurus* seems to have been towards smaller size with a relatively more robust tail having whorls of large spines. In this respect, *E. palea-ris* seemingly is primitive; *E. quinquecarinatus* is more advanced and probably is ancestral to the specialized species, *E. clarki* and *E. defensor*."

From the above it is obvious that *Enyaliosaurus* is another example of the early pre-*Ctenosaura* radiation in Central America.

MYOLOGY

An examination of the muscles has revealed that the iguanines and the Madagascanian genera exhibit two basic patterns of muscle arrangement. In *Amblyrhynchus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Iguana*, *Oplurus*, and *Sauromalus*, the cervicomandibularis is hidden beneath the posterior origin of the constrictor colli. This same group of genera, plus *Chalarodon*, has a large levator angularis oris muscle. The remaining genera, *Brachylophus* and *Dipsosaurus*, appear to form a second natural group with the cervicomandibularis muscle extending beyond the posterior margin of the constrictor colli and with a small levator angularis oris muscle present. The fact that *Oplurus* shares both characters with the larger group is an indication of its close relationship to the central iguanine stock. *Chalarodon* possesses only one of the characters and is probably the most distantly related of all the genera studied.

A few other myological characters are useful in determining relationships. The position of the adjoining borders of the intermandibularis posterior and the constrictor colli indicate a natural grouping between *Conolophus*, *Ctenosaura*, *Cyclura*, and *Sauromalus*. In these genera the borders are not connected along part of their length. In *Amblyrhynchus*, *Brachylophus*, *Dipsosaurus*, and *Iguana*, the borders of these muscles are connected for the entire length. These genera appear to have diverged away from the central stock. It is interesting to note that both *Chalarodon* and *Oplurus* have the border of the intermandibularis posterior and the constrictor colli connected for the entire length. On the basis of myology, these two genera are not iguanine but may represent the most primitive condition in the family.

The branchiohyoideus has a wide insertion on the distal end of the first certobranchial in all of the

genera except *Sauromalus*. This deviation from the iguane pattern is probably due to the unique shape of the hyoid in *Sauromalus*. Such a deviation probably represents a highly specialized condition rather than a primitive one.

The sternothyroideus is indistinguishable along its lateral border from the medial border of the sternohyoideus in all genera except *Ophurus* and *Chalarodon* where the two muscles are quite distinct. This character indicates a relationship between the two Madagascanian genera that is lacking in the iguanines.

In summary the musculature shows the iguanines to be separated into an *Amblyrhynchus*, *Conolophus*, *Ctenosaura*, *Cychura*, *Iguana*, and *Sauromalus* group, and a *Brachylophus* and *Dipsosaurus* group as determined by the position of the cervicomandibularis and levator angularis oris. The musculature further shows that *Ophurus* and *Chalarodon* form a natural grouping as indicated by the free lateral border of the sternothyroid.

Within the largest iguane group of genera; *Conolophus*, *Ctenosaura*, *Cychura*, and *Sauromalus*, there appears to be the most closely related members of the ancestral stock as indicated by each having incompletely connected borders between the constrictor colli and intermandibularis posterior muscle.

Before leaving the myology a brief discussion of *Enyaliosaurus* is pertinent. An examination of one specimen of *E. clarki* (KU 62447) shows this individual to have a large levator angularis oris, a hidden cervicomandibularis, a narrow constrictor colli, and a sternothyroideus with its lateral border fused to the sternohyoideus. The possession of these characters allies *Enyaliosaurus* closely with *Ctenosaura* and its close relatives.

Tongue

Camp (1923:374) states, "The broad, fleshy, partly smooth, partly papillate tongue of geckos and iguanids would seem histologically the least specialized and probably the more ancient type." Unfortunately this primitive tongue does not show any clear evolutionary trends between the genera of iguanines. This may be because of the low sample size used in this study.

It may be noted, however, that the poorest development of pointed papillae at the posterior end of the tongue is found in *Chalarodon* and *Ophurus*. The depth of the posterior cleft is also more shallow in the above two genera. This is another indication of the uniqueness of the two Madagascanian genera.

A single tongue from *Dipsosaurus* shows a small pointed tip at the anterior extremity of the tongue. This was not seen in larger individuals in any other genus and it may be that such a structure is a function of age and use. Older individuals may have worn

this tip away leaving the rounded tip found in the other iguanines.

Hemipenis

The study of the hemipenis was hampered by a lack of material with four genera not being represented in the series.

The hemipenis of *Brachylophus* is unique among the six genera examined as the structure is bifid rather than bulbous. The sulcus spermaticus is tightly closed and tubelike rather than an open groove as found in *Amblyrhynchus*, *Ctenosaura*, *Dipsosaurus*, *Iguana*, and *Sauromalus*. These differences may suggest a more distant relationship between *Brachylophus* and the remaining continental iguanines.

A phylogenetic chart representing the relationships between the eleven genera, as determined by the above morphological characters, is seen in Figure 37.

Iguane Distribution

Explaining the distribution of the iguanines has been especially perplexing for zoogeographers. One of the most recent statements on the subject is that of Carlquist (1965:395-396) who says, "Especially annoying to biogeographers is the presence of iguanas. Iguanas are inescapably a characteristically American family of lizards. To be sure, an iguanid (*Brachylophus*) has mysteriously reached Fiji and Tonga, on which islands the genus is endemic. But how to explain that two iguanid genera exist on Madagascar? *Chalarodon*, from the dry Southwest of the island, and *Ophurus*, with six species, are living evidence that iguanids did reach Madagascar. The best explanation seems to be that iguanas are a very ancient group of reptiles which have been extinguished on the African and Eurasian mainland, but managed, during their tenure there, to reach what were to become refuge islands for them and other creatures, Fiji and Madagascar, before they died out on the mainland." Beaufort (1951:132) and Darlington (1957:212) also consider the Iguanidae to have evolved in the Old World.

The literature on fossil lizards such as Broom (1903), Broom (1924), and Camp (1945) indicates that lizards probably originated in Africa in Triassic times. By the beginning of the Cenozoic Era, the family Iguanidae was well established in North America (Gilmore 1928, Gilmore 1941, and Estes 1964).

The family Iguanidae may also have originated in the Old World tropics. The presence of *Chalarodon* and *Ophurus* on Madagascar is evidence of a long history in the African area. Current theory indicates that the ancestral iguanids spread to Europe and Asia and eventually to the Western Hemisphere. Fossils should mark the existence of iguanids on the Eurasian land mass. Some iguanids from Europe have been de-

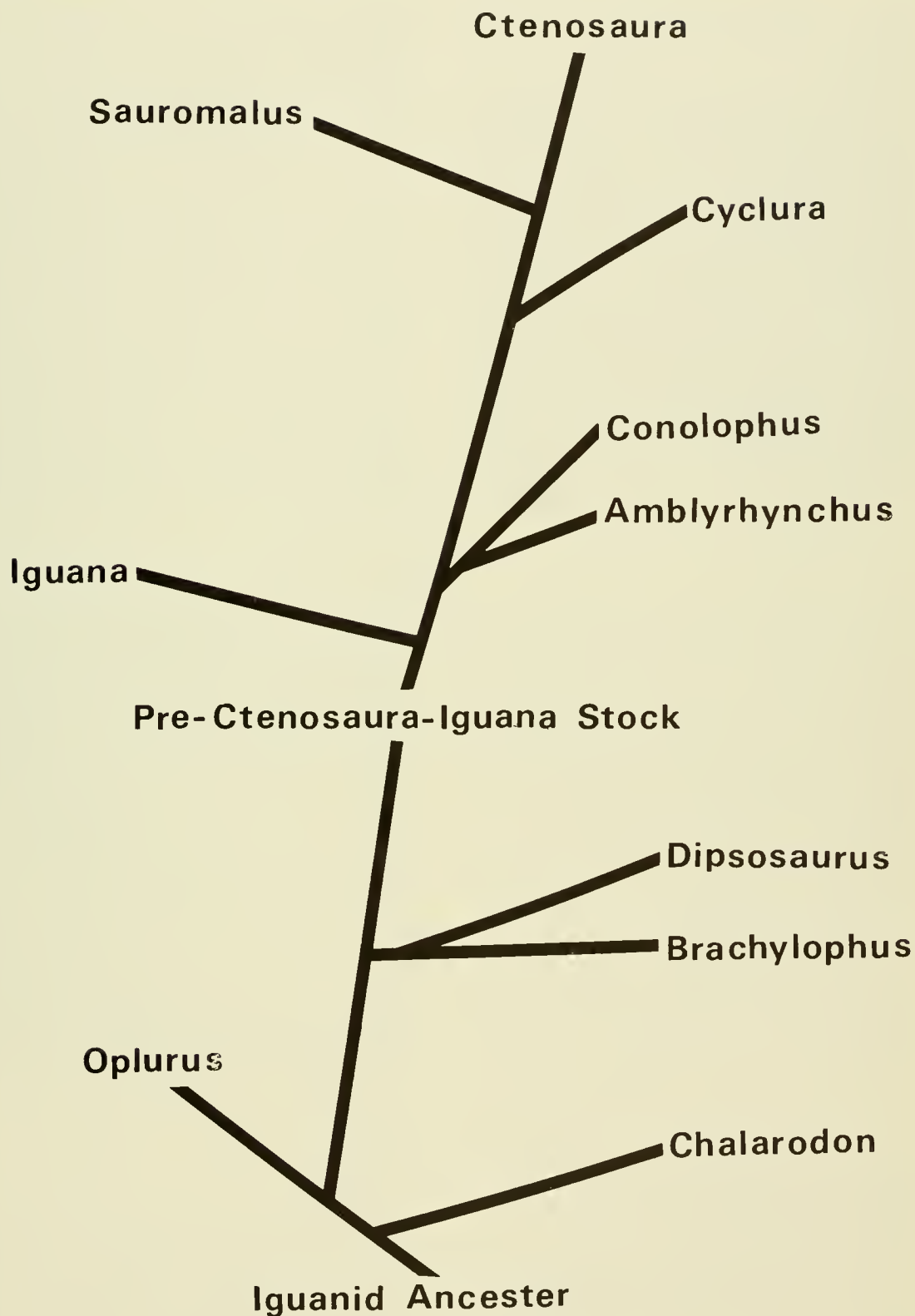


Figure 37. Phylogenetic relationships of the Madagascar Iguanidae and the genera of iguanine lizards.

scribed by Hoffstetter (1942, 1955). However, according to Romer (1968:121), these are more likely agamids. There is no fossil record for iguanids from Asia.

Regardless of the fossil record, iguanids had to reach the Western Hemisphere from the Old World tropics. One of the more logical explanations of such a migration would be for the iguanids to spread northward through Europe, invade North America via the Bering Straits landbridge, and undergo a radiation in the Western Hemisphere. The development of better adapted families of lizards in the Old World tropics could have caused the extinction of the family Iguanidae in all areas where the families competed. Only in refugia, where the iguanids were isolated from these more successful families, would the iguanids survive. Members of the family Agamidae are ecological equivalents for many iguanids and are widespread in the Old World tropics. They may have caused the elimination of the Iguanidae where the two families overlapped. It is interesting to note that there are no agamids on Madagascar where iguanids still exist. Nowhere in the world except on Fiji do iguanids and agamids live side by side.

There is an alternative method by which the Iguanidae could have reached the New World tropics. The publication of several recent papers such as Hurley, Almeida, et. al., 1967, Heirtzler 1968, Hurley 1968, Maxwell 1968, Hurley and Rand 1969, Kurten 1969, and McElhinny and Luck 1970 lend new credence to the old theory of continental drift. All of the above papers indicate the existence of a large pre-Cretaceous land mass, Gondwanaland, which fractured in Cretaceous times to form Africa, South America, Australia, Antarctica, Southern India and Madagascar.

If the Iguanidae were widespread over Gondwanaland when this continental mass fractured in the Cretaceous, they would have been separated into separate populations on each of the above land masses. Of these continental areas only the Americas and Madagascar have not been invaded by Agamidae. These two areas are also the only areas that have iguanid lizards.

Continental drift would explain why the Madagascar genera are considered primitive to the rest of the family. They are closest to the family's center of origin, and are relicts of Cretaceous times. The drift theory would also explain why the iguanine line is mostly southern and equatorial. They originated in that area in Gondwanaland and have spread little from their center of origin.

Regardless of the method of iguanine migration to the New World, be it land bridge or continental drift, we are still faced with explaining the distribution of iguanines on the oceanic islands of the Western Hemisphere.

Cychura is found in the Antilles and the Bahamas. This *Ctenosaura* derivative is widespread on the is-

lands and is endemic to the area, having migrated and evolved there when these islands were connected to the mainland.

The origin of the Galapagos Islands has been debated for many years. *Amblyrhynchus* and *Conolophus*, which are endemic to the Galapagos Islands, have been separated from the mainland genera for a long time, as indicated by their high degree of differences. If the islands are continental, these iguanids could have easily reached them. If the islands are oceanic *Amblyrhynchus* and *Conolophus* must have migrated by rafting on logs or some other floating debris.

Baur (1891:310) considered the islands to have been connected to the mainland as late as Eocene times. Heller (1903:43-44) considered the islands to be volcanic and oceanic in nature. Chubb (1933:1-25) commented extensively on the volcanic nature of the Galapagos Islands and indicated a close affinity, geologically, to Cocos Island off Costa Rica. Svenson (1948:496-498) studied the plants of the Galapagos Islands and indicated a close affinity with South America. Finally, Vinton (1951:356-376) proposed a partial or complete land bridge from Costa Rica through Cocos Island to either a connection with the islands or terminating in a close proximity to the Galapagos land mass that later sank forming the present islands. This land bridge would have been developed in Mid-Tertiary time and would have provided means whereby turtles and iguanids could have gotten close enough to the islands to raft successfully. As the land bridge never attached to the Galapagos Islands, these oceanic islands would have retained a considerable degree of uniqueness. Regardless of land connection or not, a pre-*Ctenosaura*-*Iguana* ancestor apparently did make the trip and later diverged into modern day *Amblyrhynchus* and *Conolophus*.

The problem of *Brachylophus* on Fiji and Tonga Islands is to us the most perplexing problem in iguanine distribution. If the iguanines were widespread in the world during late Mesozoic-early Cenozoic times and were widely scattered on the Gondwanaland continental nucleus, they should have occurred in Australia and Asia after the fracturing of that nucleus. From Australia or Southeast Asia it is a short trip by rafting to the Fiji and Tonga Island groups. If such a trip were accompanied by iguanid elimination on the Asian and Australian land masses by agamids, *Brachylophus* would be left isolated on Fiji and Tonga.

Two factors disrupt the plausibility of this theory, however. If iguanines were widespread and gave rise to the Fiji and Tonga populations of *Brachylophus* via Asia and/or Australia, one would expect to find other relict populations on other Pacific Islands such as New Zealand, New Guinea, the Solomons, the Philippines, and Indonesia. These islands are all inhabited by agamids which could have eliminated

Brachylophus and other iguanines. Unfortunately the fossil record does not provide evidence of any Far Eastern Iguanidae, and we find today that agamids and *Brachylophus* do exist together on Fiji. This modern coexistence may be the result of *Brachylophus* or the agamids being recent invaders of the islands rather than long term residents.

A second fact disrupting the Far Eastern Theory for the origin of *Brachylophus* is the relationship of *Brachylophus* to *Dipsosaurus*, the North American iguanine. Did *Dipsosaurus* also raft from the Far East to North America? It seems highly unlikely. A more plausible explanation for the problem is that a *Brachylophus-Dipsosaurus* complex existed in the Western Hemisphere, closely related to the existing iguanine complex. *Brachylophus* in the South Pacific is probably the result of a few individuals that accidentally rafted on floating debris to the Fiji and Tonga Island groups and a Northern survivor of this complex has evolved into the modern *Dipsosaurus*. Such a hazardous journey by log raft needs to occur

only once with a gravid female to produce a viable island population.

Sauromalus represents the most northward extension of the iguanine line. Gilmore (1928:27-28) described the teeth of *Parasauromalus olseni* from the Middle Eocene, Wind River Formation of Fremont County, Wyoming. This fossil form may represent the ancestral stock of *Sauromalus* and indicates the withdrawal of the modern *Sauromalus* from what once was a more extensive and northern range. According to Savage (1966:722-723), North and South America were connected in Paleocene and Pliocene times. The pre-*Sauromalus* stock may have invaded North America in Paleocene times before the land bridge was broken. This *Sauromalus* stock may have been separated from the *Ctenosaura* stock from Eocene to Pliocene times and evolved and diverged far enough from the parent stock to allow *Ctenosaura* to reinvade southern North America in late Pliocene times and overlap the *Sauromalus* range without competing ecologically.

CONCLUSIONS AND SUMMARY

The problem of phylogenetic relationships within the iguanine phyletic line and the Madagascar iguanids have been investigated in order to explain the discontinuous distribution exhibited by the members of the family Iguanidae. Owing to inconclusive results from cytology and histological methods, the comparative morphology of the anterior osteology, myology, tongues, and hemipenes were used to determine relationships.

An examination of the above structures of the members of the iguanine phyletic lines and a comparison with the Madagascar iguanids indicates the following: (1) The Madagascar genera *Chalarodon* and *Oplurus* appear to be more closely related to each other than to other iguanid genera. (2) The Madagascar genus *Oplurus* is most closely related to the iguanine line of evolution. (3) *Ctenosaura*, *Cyclura* and *Iguana* represent the main ancestral stock of iguanines in the Western Hemisphere. (4) *Cyclura* is probably an early descendant of the *Ctenosaura* an-

cestral line. (5) *Iguana* and *Ctenosaura* evolved from a common ancestral stock. (6) *Sauromalus* is a northern derivative of the *Ctenosaura* ancestral line. (7) *Conolophus* is probably an early invader of the Galapagos Islands and is derived from the pre-*Ctenosaura-Iguana* iguanine ancestral stock. (8) *Amblyrhynchus* is a close relative of *Conolophus* and may be derived directly from a *Conolophus* ancestor. (9) *Brachylophus* is a derivative of the pre-*Ctenosaura-Iguana* ancestral stock and probably rafted to the Fiji and Tonga Islands from tropical America. (10) *Dipsosaurus* is more closely related to *Brachylophus* than any other iguanine and represents the northern extension of that generic complex. (11) The Madagascar iguanids and the Western Hemisphere iguanines were probably separated in post-Cretaceous times by continental drift which is thought to have resulted in a fracturing of Gondwanaland and the formation of Australia, southern India, Antarctica, Africa, Madagascar, and South America.

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LAND USE IN WAH WAH AND PINE VALLEYS, WESTERN UTAH

by
Joseph R. Murdock
and
Stanley L. Welsh



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Frontispiece A. Rabbitbrush, halogeton, and other shrubs, southeast quarter of Wah Wah Valley.



Frontispiece B. Galleta grass and desert shrubs, southwest quarter of Pine Valley.

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LAND USE IN WAH WAH AND PINE VALLEYS, WESTERN UTAH¹

by
Joseph R. Murdock²
and
Stanley L. Welsh³

ABSTRACT

This is a review of the use of public lands in Wah Wah and Pine Valleys in western Utah for grazing of livestock, mining, and other private enterprises. The total area of the two valleys is approximately 1,440 square miles of which about 30 square miles are privately owned. From the time grazing of domestic livestock was initiated in the 1870's and 1880's until 1934, the land was free public domain and was grazed on a first-come, first-served basis. Passage of the Taylor Grazing Act in 1934 ended free use of public lands. Existing evidence indicates that by 1934 the grazing base was badly depleted. In the period from

1934 until the early 1950's, the Bureau of Land Management policies resulted in a general evaluation of range conditions; and since the 1950's policies such as reclamation of pinyon and juniper lands by clearing and seeding have made possible the better distribution of livestock on a seasonal basis and the determination of proper stocking rates. Adjudication of Pine Valley in 1956 and Wah Wah Valley in 1962 have allowed for general improvement of range conditions. Certain abuses of public lands still exist as evidenced by poor control of road building, mining exploration, and predator control practices.

INTRODUCTION

Wah Wah and Pine Valleys are located in western Millard and Beaver Counties, Utah, in the southeastern portion of the Great Basin (Map 1). To the east of Wah Wah Valley lie the San Francisco Mountains and west of Pine Valley the Needle Mountains. The valleys average about 50 miles in length and 10 to 20 miles in width. The combined area is about 1,440 square miles. About 1,240 square miles of land in the region is under Federal control. Of this total, 87 square miles is included in the Forest Service, Intermountain Forest and Range Experiment Station, Desert Experimental Range, and about 1,153 square miles are controlled by the Federal Bureau of Land Management. The remainder of the region is owned by the State of Utah (about 170 square miles) or is in private ownership (about 30 square miles). Land in the vicinity of Indian Peak designated as Indian Reservation has been purchased by the Utah State Fish and Game Board (Hancock, 1969) and is included in the State lands total.

The climate of the region is marked by great temperature extremes, scanty precipitation, and strong, drying winds of almost daily occurrence. The average

annual precipitation in the center of Pine Valley over a 24-year period is only 6.1 inches (Holmgren, 1969). The mountains receive heavier amounts (e.g. 17.9 inches annually on the Needle Range) and are snow covered each year, but the valley bottoms are seldom snow covered for more than a few days or weeks. Daily and seasonal fluctuations in temperature are great, with extremes of 100°F in summer and -35°F in winter (Stewart, et al., 1940).

Springs and streams are few in number and are located in the mountains above the valley floors. Permanent streams are small and sink before they reach the valley bottoms.

Vegetation is composed of species typical of the Northern Desert Shrub Biome. The valley bottoms are occupied by sparse shrub and shrub-grass vegetative types (Map 2). Major plant species are shadscale, winterfat, budsage, black sagebrush, big sagebrush, rabbitbrush, horsebrush, and grasses. At elevations above the shrub types and interfingering downward with them is the juniper-pinyon community. This is the most important woodland type covering thousands of acres in the foothills and mountains. Various

¹This study was made possible by a grant from the Public Land Law Review Commission to the Rocky Mountain Center on Environment, Denver, Colorado.

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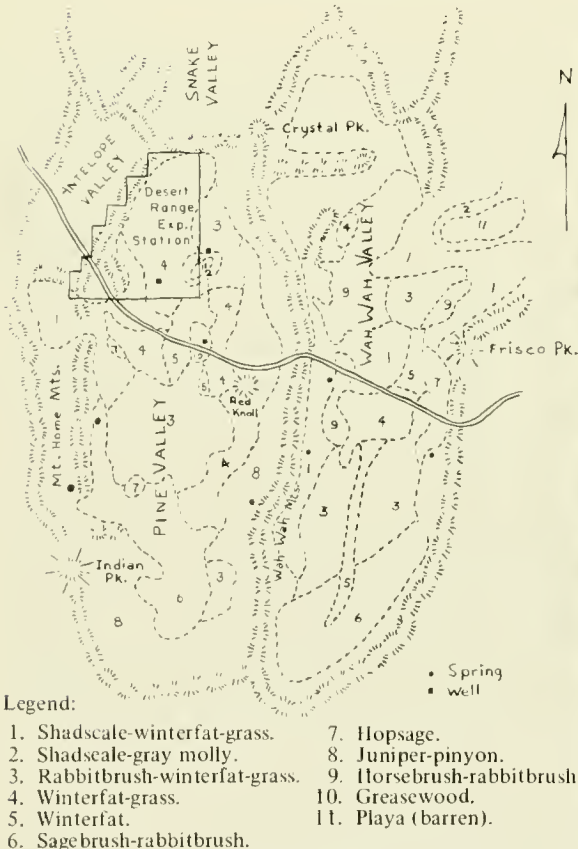


Map 1. Location of Great Basin Desert.

grasses are abundant in the subtypes of this community. Scattered stands of Douglas-fir, white fir, bristlecone pine, ponderosa pine and aspen occur at higher elevations in the mountains.

In this setting was impressed the grazing of livestock and the attendant road building, fence construction, water development, and other activities which were to result in long-lasting changes in vegetation, scars on the landscape, soil erosion, and changes in water runoff.

The region has been used primarily for winter grazing of livestock, but some portions were utilized throughout the year and others only in the summer. The winter range is dry, for there are only a few, small, widely dispersed springs, but the twigs of dormant shrubs are palatable and nutritious, and the dry grasses provide energy. Light snow cover provides water for the animals but seldom diminishes the availability of forage. As snow recedes from the valley and benches, sheep can be driven to the hills where drifts remain longer, and the early sheepmen found that by following the snow, which is used for stock water, they could use the desert ranges in the winter. As sheep populations grew, it became necessary to trail them farther into the deserts for feed. Through cooperative efforts, the sheepmen developed the more



Map 2. Vegetation types in Wah Wah and Pine Valleys (after Stewart et al., 1940).



Fig. 1. Cemetery at Wah Wah Springs, Beaver Co., Utah. Edwin Saxton Squire epitaph. "Green is the turf above the husband of my better days, none knew thee but to love, none named thee but to praise."

productive springs and built catchments for rainfall runoff to provide water for animals moving over the

driveways to and from their increasingly distant winter ranges (Holmgren, 1965).

ENVIRONMENTAL IMPACT AND PROBLEM ORIGINS

Historical

The historical background of Pine and Wah Wah Valleys might be characterized by an epitaph from a tombstone (Fig. 1) at a cemetery at Wah Wah Springs on the west side of Wah Wah Valley. It states: "Green is the turf above the husband of my better days, none knew thee but to love, none named thee but to praise." The turf, if it ever existed, was probably seldom green, but the vegetation was the basis upon which settlements were established, and a way of life was developed.

The two valleys have not received the same amount or type of utilization. Wah Wah Valley is situated more closely to Milford and other population centers than is Pine Valley. Ore was discovered in the San Francisco Mountains in the late 1800's, and the mining town of Frisco arose, functioned, and failed upon removal of the rich ores (Fig. 2). Frisco had a population of some 4,000 during its heyday and was a major receiver of meat and other products such as charcoal from neighboring Wah Wah and Pine Valleys. It was also the railhead for the Utah Central Railroad. The railroad was later extended from Frisco to the ore processing town of Newhouse (Fig. 3) which was built on the slopes of the eastern side of Wah Wah Valley. Water was piped from Wah Wah Spring (Fig. 4) on the west side of the Valley eastward to Newhouse. A sheep-shearing shed and corrals were built adjacent to Newhouse (Fig. 5). The sheds in which some 200,000 head of sheep were reported to have been sheared annually, are still standing but unused. Both Frisco and Newhouse survive only as mine or slag dumps (Fig. 6), foundations (Fig. 3) and a cemetery (Fig. 7).

No such concentration of human activity of a corresponding nature occurred in Pine Valley. In addition, Pine Valley had fewer adequate stock watering sites and was not utilized as heavily or as soon as was Wah Wah Valley. Wah Wah had been grazed for about 70 years prior to 1940 (about a century now) whereas Pine Valley had been grazed for only about 50 years prior to that time (Stewart, et al., 1940). Early grazing was by cattle only (Stewart, 1940; U.S. Dept. of Interior, 1964). Sheep grazing in large numbers occurred in Wah Wah Valley in the late 1880's where they were grazed along with cattle already present. Cattlemen in Pine Valley succeeded for about another decade in keeping sheep from that valley.

During the period from 1910 to 1915 forage utilization by livestock was judged to have become seri-

ously destructive to vegetation in Pine Valley (Stewart, et al., 1940). Forage use in Pine Valley during the years from 1915 to 1934 reportedly exceeded proper use in nearly the same degree as was common in Wah Wah Valley from about 1885 to 1934 (Stewart, et al., 1940). Changes in vegetation during the extended period of heavy grazing by sheep and cattle resulted in death or reduction of vigor of those plants most readily eaten by livestock (e.g., budsage, black sagebrush, winterfat, and grasses) and in the increase of plants belonging to species which were avoided by livestock because of their being unpalatable (rabbit-brush), moderately palatable (shadscale), or poisonous (horsebrush) (Deming, 1952; Stewart, 1940).

Despite the increase in numbers of some species, reduction of total plant cover also resulted from the heavy grazing pressure (McGuire, et al., 1937). Because of this, erosion proceeded at an accelerated rate, and the Pine - Wah Wah Valley region was designated as being "moderately" to "severely" eroded (Deming, 1952). As early as 1936, it was noted that the pedestaled nature of many desert plants, especially winterfat, showed that from one to six inches of soil had been removed from below the crowns since their establishment. This was true regardless of age of plants. Some were only a few years old and were pedestaled as much as the old plants, indicating recent erosion (Stewart, 1940). Embryonic sand dunes were also noted (Deming, 1952; Stewart, 1940).

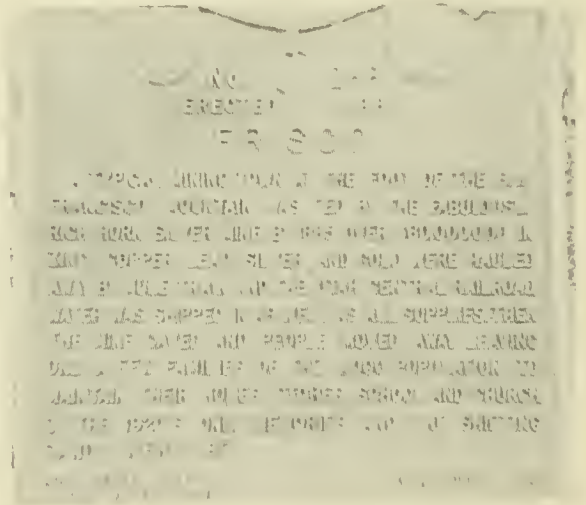


Fig. 2. Daughters of Utah Pioneers Monument at the old townsite of Frisco, Utah, Beaver Co., Utah.

The drought of 1934 has been discounted as a major factor in the decline of vegetation and in soil erosion, by various writers (Stewart, 1940, pp. 290-291; Deming, 1952). It has been noted that there was a drought from 1897 to 1904 which was of equal or greater severity than that of the early 1930's. Yet, "fat sheep were marketed on the desert range in mid-winter during the decade 1895 to 1904, according to the testimony of resident stockmen" (Stewart, 1940, p. 291). However, as early as the year 1928, more than 4,200 head of sheep out of a band of 5,000 starved to death in Pine Valley (U.S. Dept. of Interior, 1956) well before the drought of the 1930's became severe. "The evidence is that in the early days, the damaging effect of acute shortage of moisture in drought years was offset by moderate utilization, which permitted restoration of the normal growth and nutritional function of the range plant" (Stewart, 1940).

Another change in plant cover demonstrated in many parts of Utah was the invasion of juniper and pinyon from the mountain slopes downward onto the deep alluvial soils of the valleys. Neither pinyon nor juniper are eaten preferentially by grazing animals, and both increase and spread when other plants more readily eaten are grazed excessively. Photographs taken at the townsite of State Line (Figs. 8 and 9), a mining camp in the White Rocks Range at the south

end of Hamblin Valley, Iron Co., Utah, in 1909 and 1959 show a striking change in the juniper-pinyon woodland. The trees have increased in number on the hillsides and have extended their range into the lowlands. Even the 1909 photograph demonstrates that the migration was already well advanced, adding support to the idea that native vegetation is rather quickly transformed under heavy grazing pressures. Hamblin Valley is the next valley west of Pine Valley, and the State Line site is comparable to portions of the south end of Pine Valley now occupied by juniper and pinyon also.

Thus, by the early 1930's the public lands under the jurisdiction of the General Land Office were in a generally poor state with regard to vegetation and soil stability.

Public Lands—1933 to Present

From the time when grazing of domestic livestock began in Pine and Wah Wah Valleys in the 1870's and 1880's until 1934, the land was free public domain. It was grazed on a first-come, first-served basis. When the vegetation in one area was depleted another was sought to take its place. However, by the turn of the century almost every part of the range suitable for livestock was being grazed and expansion into new territory became impossible (Hutchings, 1954). Free



Fig. 3. Ghost town of Newhouse, with home ruins in background and smelter ruins right foreground. Wah Wah Valley, Beaver Co., Utah.



Fig. 4. Privately owned Wah Wah spring flows approximately two second feet and irrigates about 40 acres of land. The only systematically irrigated land in Pine or Wah Wah Valleys, Wah Wah Valley, Beaver Co., Utah.

use of ranges in the arid lands ended when they were brought under management following establishment of the Desert Experimental Range in 1933, and following the enactment of the Taylor Grazing Act of 1934 (see 48 Stat. 1269, 43 U.S.C. §§ 315-3150-1).

Desert Experimental Range

It is impossible to adequately assess the total numbers of animals grazed in Pine and Wah Wah Valleys prior to 1930 or to estimate the carrying capacity (i.e. the total animal-unit months of forage available from a tract of forage land in a given period) of the range. It was possible, however, to detect that the vegetation was in poor condition and that its value for grazing was greatly reduced (McGuire, 1937; Menzies, 1935; Stewart, 1940). Concerned Forest Service people with knowledge of grazing practices initiated the establishment of the Desert Experimental Range in 1933. The range was fenced around the periphery and divided into pastures where experiments in differential grazing and management were established. The most modern methods were utilized in determining vegetation quality and quantity, animal usage, and other data. Cooperators were allowed to graze sheep and cattle in pastures as provided by an overall experimental design (Hutchings, 1954).

A study of 23 years of controlled grazing at the Desert Experimental Range was undertaken in 1958 (Harper, 1959). In that study it was concluded that the most palatable species (i.e. budsage and winterfat) have increased and the less palatable shadscale has decreased in relative importance during the 23-year period under all grazing treatments, except on those heavily grazed in springtime. The same type of improvement was noted for black sagebrush in 1964 (U.S. Dept. of Agric., 1965) and for budsage in 1966 (Wood, 1966). Galleta grass increased in relative importance in all plots which supported that grass in 1935 (Harper, 1959).

It should be noted, however, that the heaviest grazing treatment at the Desert Experimental Range (nine acres per Animal-unit month, or AUM) was thought to be less than that employed by livestock operators in the remainder of Pine and Wah Wah Valleys (roughly six acres per AUM as extrapolated from adjudication figures). An AUM is defined as the amount of feed necessary to sustain one cow or five sheep for a period of one month (U.S. Dept. Interior, 1964, p. 3). Moderate grazing pressures at the Range were stocked at the rate of 13 acres per AUM and light at 18 acres per AUM.



Fig. 5. Newhouse shearing sheds and corrals. As many as 200,000 head of sheep were reported to have been sheared here during a single year. Wah Wah Valley, Beaver Co., Utah.



Fig. 6. Slag dump at the town of Newhouse in the foreground. Pipeline through present-day ranch continuing to the town from Wah Wah Springs is evident on valley floor. Wah Wah Valley, Beaver Co., Utah.

Under the experimental treatments at the Desert Experimental Range, the vegetation has been improved and maintained at a high level, and at the same time, livestock grazed there have provided greater economic return in the form of increased yield of wool, lambs, and healthy breeding stock (Hutchings, 1954, 1958).

That the Bureau of Land Management was aware of the studies at the Desert Experimental Range is evident from statements made in 1952 (Deming, 1952, p. 31), when it was noted that "similarity of vegetation and environment makes the results of experimental studies of management of winter sheep ranges applicable in the Milford unit with little adjustment."

Bureau of Land Management

Prior to 1934, the lands were under the jurisdiction of the General Land Office which was constituted to dispose of public lands, rather than to manage their use. The Taylor Grazing Act authorized the Secretary of the Interior to establish grazing districts from the public domain which in his opinion were chiefly valuable for grazing and raising forage crops. The Secretary was authorized to issue permits for the grazing of livestock on the grazing districts, with preference being given to landowners engaged in the livestock business. He was directed to make provision for the protection, administration, regulation, and improvement of such grazing districts as may be created and to make such rules and regulations and do any and all things necessary to accomplish the purposes of the Act and to insure the objects of such grazing districts, namely, to regulate their occupancy and use, to preserve the land and its resources from destruction or unnecessary injury, and to provide for the orderly use, improvement, and development of the range. He was also authorized to continue the study of erosion and flood control and to perform such work as might be necessary. The Secretary was further directed to specify from time to time numbers of stock and seasons of use.

The Taylor Grazing Act provided for cooperation with other departments of the federal government and with State agencies and local associations engaged in conservation or propagation of wildlife. Furthermore, in order that the Secretary of the Interior might have the benefit of the fullest information and advice concerning physical, economic, and other local conditions in the several grazing districts, it was instructed that there should be an advisory board of local stockmen in each grazing district. These boards were empowered to offer advice on applications for grazing permits, proposed rules and regulations, the seasons of use and carrying capacity of the range, and any other matters affecting the administration of the district.

The Grazing Service, acting under the authority of the Taylor Grazing Act of 1934, began the task of managing a range which was badly depleted according to available evidence. The use of the region as grazing land for livestock was dictated long before the Taylor Grazing Act was passed, and the first business of the Grazing Service was to determine the extent to which grazing privileges should be allowed. The district (Pahvant Grazing District—Utah Number 3), of which Pine and Wah Wah Valleys are a part was established in 1935 and subdivision of the district into management units occurred in 1937 (Deming, 1952). By 1936 livestock operators had received licenses for specific numbers of livestock, evidently based in large part on previous practices of the operators.

Comprehensive range surveys to determine the capacity of the range to support grazing animals were not carried out on the Milford Unit, of which Wah Wah Valley is a part, prior to 1950 (Deming, 1952), and none is known to have been made in Pine Valley prior to that time either. However, "several estimates were made of carrying capacity by applying rule of thumb methods based on advisory board recommendations" (Deming, 1952). As early as 1936 there was a tacit recognition that overstocking existed to the extent of about 30 percent, and that carrying capacity should be set at about 8.65 acres per AUM (Deming, 1952).

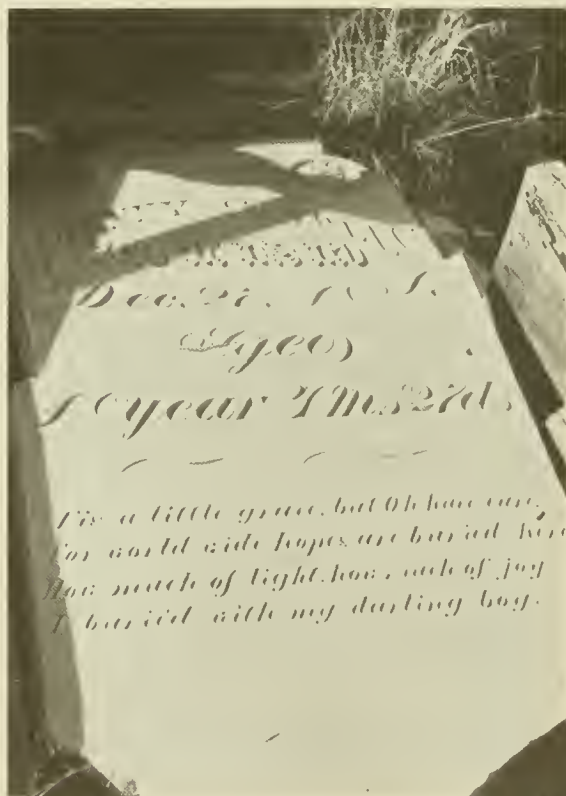


Fig. 7. Johnny Staples grave marker, 27 December 1881. This grave is typical of many in a state of decadence. Frisco Cemetery, Beaver Co., Utah.



Fig. 8. Townsite of State Line taken in 1909, Iron Co., Utah. Note sparsely scattered, small trees near town and on slopes in background.



Fig. 9. Townsite of State Line taken in 1959, Iron Co., Utah. Much less bare area is evident between trees in just 50 years of reduced competition with forage species due to grazing.



Fig. 10. Utah State Department of Fish and Game pond partially silted in by a flood. Increased water supplies are the result of cleared lands above. Pond has provided fish up to 18 inches long. Indian Creek, Indian Peak, Pine Valley, Beaver Co., Utah.



Fig. 11. Sheep bedground. The dark area on the knoll in the center background and is dominated by Russian thistle. Antelope Valley, Desert Experimental Range, Millard Co., Utah.



Fig. 12. Watering trough and tank east of Wah Wah Spring. Water is available during winter for livestock but unavailable for wildlife in other seasons. Wah Wah Valley, Beaver Co., Utah.



Fig. 13. Woods' cabin and well. The effect of high concentrations of livestock is evident for several hundred yards in the immediate vicinity. Pine Valley, Beaver Co., Utah.



Fig. 14. A highlined juniper indicating severity of use by livestock. This could have occurred in a severe winter or by heavy use during long periods of grazing. The effect is usually rather permanent. North end of Pine Valley, Millard Co., Utah.



Fig. 15. Russian thistle and scattered shrubs on terrace of ancient Lake Bonneville. Trees indicate the termination of a pipeline. South end of Wah Wah Valley, Beaver Co., Utah.



Fig. 16. A halogeton stand, made possible by overuse of the more palatable species that previously occupied this area. BLM land. North end of Pine Valley, Millard Co., Utah.



Fig. 17. Stock watering pond and adjacent depleted land. Pipeline to Newhouse evident on right background. Wintch Ranch, Wah Wah Valley, Beaver Co., Utah.



Fig. 18. Manure and devastated vegetation in corner of pasture. BLM Land in north end of Pine Valley, Millard Co., Utah.



Fig. 19. Fence-line contrast. BLM land on right dominated by halogeton. Desert Experimental Range on left dominated by native shrubs and grasses. North end of Pine Valley, Millard Co., Utah.

The Milford Unit recorded some 75,141 sheep and 952 cattle in 1936, but the number of AUM's is unknown due to continued common use practices by the operators. Between 1936 and 1950 the number of sheep declined to 58,577, but the cattle numbers increased to some 2,137. Animal-unit months are recorded for all years between 1939 and 1950. In that 12-year period the average number of AUM's for both cattle and sheep was 87,062. However, in 1950 it was recognized that for the Milford unit, "because of acreage differences in various tabulations, it appears that an estimated grazing capacity of approximately 70,000 AUM's has been accepted as a working basis or goal" (Deming, 1952). Thus, the average stocking rate in the Milford Unit from 1939 to 1950 was recognized to exceed estimated carrying capacity of the range by about 17,000 AUM's.

Pine Valley was adjudicated (i.e. the procedures of determining forage production and its equitable apportionment among livestock operators in a grazing unit) in 1956 and Wah Wah Valley in 1962. The total number of AUM's allowed following adjudication was 27,389 in Pine Valley and 29,611 in Wah Wah Valley (or about 12.9 acres per AUM based on estimated 738,000 acres of Public lands in the two valleys). These figures represent an average reduction of 32.8 percent for Pine and 53.0 percent for Wah Wah (Bayless, 1969; U.S. Dept. of Interior, 1956). Although detailed surveys of the vegetation have not been made since adjudication, there is evidence of general vegetation improvement (Bayless, 1969; Brough, 1969; Burt, 1969; Cropper, 1969; Holmgren, 1965) on the federal lands.

ENVIRONMENTAL CONSIDERATIONS

With many thousands of acres of juniper-pinyon woodland available for management, it would seem that further emphasis needs to be placed on evaluation of their highest potential use. Pinyon is valuable as firewood, as Christmas trees, and as a producer of edible seeds. Juniper is cut for fence posts. The harvest is regulated by the Bureau of Land Management. However, information on highest potential use and sustained yield production is unknown. It seems that management policies are necessary.

Evidently, further destruction of the grazing resource base can be avoided by following regulations and policies now in effect. However, there are problems of long standing which are not solved entirely by changes in AUM's or by reseeding operations. Some of the problems are illustrated by observing the permanent influence of sheep bedgrounds (Fig. 11), where Russian thistle, a weedy, Old World introduction, now occupies these bedgrounds even after 30 years of not being used for this purpose. Where watering troughs (Fig. 12), shearing sheds (Fig. 5), or

There is evidence that the juniper-pinyon woodland continued to expand under the management practices of the 1930's and 1940's. Useable forage production on much of the woodland was estimated to be less than 50 pounds per acre. In the late 1950's and early 1960's, a program was initiated by the Bureau of Land Management in cooperation with the Soil Conservation Service and certain of the private livestock operators for improving suitable lands covered with juniper and pinyon. The trees were removed and the lands were planted to grass. The resulting forage production represented a 10- to 100-fold increase in useable forage (Brough, 1969; Burt, 1969). This increase in forage production has made it possible to initiate changes in the season of use for some of the livestock operators. Now there is available high quality forage at higher elevations which allows relief for the vegetation in valley bottoms during the summer season. The Bureau has reseeded some 14,500 acres of juniper-pinyon woodland.

It is interesting that following the reseeding of the woodland type there was an increase in water yield from those lands. Streamflow in adjacent tributaries increased and the season of flow lengthened. This is true not only on the Federal lands, but also of Utah State lands where 5,500 acres of juniper-pinyon woodland have been cleared and planted to browse plants for wildlife. The improved water regimen has made it possible to construct recreation pools (Fig. 10) for fishing purposes, and has increased the amount of water available for livestock and for wildlife (Hancock, 1969).

dwellings and corrals for base operation of ranches (Fig. 13) have been located there is evidence of low quality (Figs. 14 and 15) or even poisonous plant (Fig. 16) introductions into the area. These sites are not only detrimental to good grazing practices, but are unsightly blights on the landscape (Figs. 17 and 18). These evidences of vegetation response to man's activities further emphasize the fact that the plant community or ecosystem achieves a complicated balance only after many years of change. The balance is so delicate that whenever a deteriorating influence such as overgrazing or trampling is introduced the effect is immediate and of long duration. The incidence of high animal concentrations centrally located associated with the practice of trailing sheep to a water trough or shearing sheds is a practice that can be or has been changed. Certain practices and structures are necessary if grazing is to continue, but some detrimental practices should be altered or abandoned altogether. Even though the general quality of forage plants is improving, there are still differences between

vegetation under controlled grazing within the Desert Experimental Range and the Public Lands outside (Figs. 19 and 20) where grazing pressure has been much heavier. Vegetation changes which have resulted from poor grazing practices certainly point the way for improvement in quality that seems so necessary.

Less desirable and low quality or poisonous forage plants can be replaced by species that will improve the habitat for livestock as well as wildlife. Enlightened management practices, such as the adjudications of 1956 and 1962, can result in betterment of rangelands (Fig. 21) and rehabilitation through removal of undesirable species; and reseeding (Figs. 22 and 23) can also result in better forage production.

By maintaining good management practices the intrusions of undesirable or poisonous Old World plants can be kept at a minimum. Prior to 1934, cheat grass, Russian thistle, and horehound were introduced to Utah and found adequate habitat in our grazing lands. Between 1934 and the present, the poisonous plant halogeton spread throughout our winter sheep ranges, and another poisonous plant, henbane, was noted in Pine Valley in 1962 (Holmgren, 1965) and is spreading along sheep bedgrounds and trails.

The practices of water development to include wildlife as well as livestock have been largely neglected. Many water development programs have been principally concerned with providing livestock with water. The development of watering troughs and storage tanks close to the water source, or the practice of piping water to remote locations has resulted in making water less available for many wildlife species. Inasmuch as water development is the key to increase in numbers of antelope and probably of other species as well, it would seem that provisions could be made for concurrent use of water by both wildlife and livestock (Fig. 24).

Continuous, poor road-grading practices have resulted in year after year lowering of the roadbed below the level of the adjacent terrain. A windrow is often produced on the down-slope side of the road (or on both sides) and has changed the roads into "canals" (Figs. 25 and 26) running along and often downhill for long distances. Runoff from excessive rainstorms collects and contributes to erosion of great magnitude. During winter storms, the roads become drifted in and impassable whereas the surrounding areas are free from snow. With unnatural water diversion the vegetation has been altered, often with a complete change of dominant species in many areas in Pine and Wah Wah Valleys. The maintenance of roads on Federal Lands is done by the counties which are subsidized by the state which in turn receives Federal Funds for this purpose (Keough, 1969).

Proper grazing practices may make it necessary to build access roads, fences, corrals, and certain ranch buildings. The Bureau of Land Management has poli-

cies regulating the location and construction of buildings and other structures, but some facilities leave much to be desired (Fig. 13). State and Federal policies often lack consistency. State land policy allows for the construction of lambing sheds on land contiguous to Federal Lands even though they are not allowed on Federal lands (Fig. 27). The effects of such a structure on vegetation of adjacent Federal Lands, even though it is built on State Lands, are the same. Animals are concentrated and vegetation is destroyed. The same is true for such structures on private property surrounded by Federal Lands.

Nongrazing practices that have contributed to environmental changes are those resulting from mining and mining-related enterprises (Fig. 6). Abandoned mine buildings and machinery (Fig. 28), old coke ovens (Figs. 29 and 30), a smelter (Fig. 6), a foundry (Fig. 31), the railway, townsite, homesite (Fig. 32), and graveyard (Fig. 7) are all evident in the area considered in this study. Modern mining exploration is evident also. Enlightened range management practices do little good if it is possible to explore for minerals in any manner whatever without regard to the Bureau of Land Management's supposed regulation of Federal Lands. Here State and Federal regulations differ. To explore for minerals on State Lands requires a permit from the State Land Board (Crystal, 1969). However, any part of the Federal Lands can be explored by bulldozer, plow, shovel, or any other means as long as State filing laws are followed (U.S. Dept. of Interior, 1964). The Bureau of Land Management finds out about the exploration only after the fact.

Attempts at ranching and farming have also left their marks on the landscape in the form of fields (Fig. 33), abandoned farmsteads (Fig. 34), springs (Fig. 4), and cemetery (Fig. 1). Many of the abandoned structures are of significant historical value and are in need of preservation. Others are eyesores and should be obliterated.

Although there is a stated policy by the Bureau of Sport Fisheries and Wildlife concerning the animal damage control programs, it appears that certain indiscriminate killing of questionable problem animals does occur (Durrant, 1952, p. 449). This problem is compounded by both private and government trappers working a region without correlation of results. A total list of animals killed and dumped along a crossroads junction for all to see on December 13, 1969, included two badgers, two bobcats, five gray fox, one kit fox, and one long-eared owl (Fig. 35). These were apparently taken by a private individual, but the region is also marked as containing cyanide devices and the poison "1080" (Ridgeway, 1969).

If "it is the objective of the Bureau to reduce animal depredations as selectively as possible" (U.S. Dept. of Interior, 1964, p. 5), then a lack of proper execution of the policy occurs at the local level. Federal, State, and County programs need further



Fig. 20. BLM land on left of fence with unpalatable rabbitbrush as the dominant vegetation. Desert Experimental Range on right with highly preferred black sagebrush as dominant. Antelope Valley, Millard Co., Utah.



Fig. 21. Galleta and Indian ricegrass with a shrub mixture. This photo gives evidence of high potential productivity where grazed every other year in the spring. Desert Experimental Range, Pine Valley, Millard Co., Utah.



Fig. 22. Reseeding in cleared juniper-pinyon woodland on BLM land. Useable forage increased 10 to 100 times. South end of Wah Wah Valley, Beaver Co., Utah.



Fig. 23. Successful reseeded area of intermediate wheatgrass. Seeds were drilled in after chaining, windrowing, and burning of trees. Noncleared area provides cover for wild game. South end of Pine Valley, Beaver Co., Utah.



Fig. 24. Permanent pond available for use by both livestock and wildlife, near Wah Wah Spring, Wah Wah Valley, Beaver Co., Utah.



Fig. 25. Roadway diversion of natural drainage causing change in vegetation type, Four-wing saltbush on left and scattered shadscale on the right. South central Pine Valley, BLM Lands, Beaver Co., Utah.



Fig. 26. Halogeton and windrow lined roadway. The road now acts as a "canal" during periods of heavy rain. North end of Wah Wah Valley, Millard Co., Utah.



Fig. 27. Lambing shed and corrals on State Lands in south end of Wah Wah Valley, Beaver Co., Utah.



Fig. 28. Abandoned mine buildings and mine dump, Frisco, Beaver Co., Utah.



Fig. 29. Wah Wah Valley from Kiln Spring showing young juniper invasion onto lower slopes. Beaver Co., Utah.



Fig. 30. Charcoal kilns at Kiln Spring, Wah Wah Valley, Beaver Co., Utah.



Fig. 31. Slag pile from old iron works. West side of Wah Wah Valley, Beaver Co., Utah.



Fig. 32. Abandoned buildings, Squaw Spring, Wah Wah Valley, Beaver Co., Utah.



Fig. 33. Wintch Ranch alfalfa field. About 40 acres irrigated from Wah Wah Spring. Wah Wah Valley, Beaver Co., Utah.



Fig. 34. Abandoned farmstead in foreground with modern corral in background. Wah Wah Valley, from Wah Wah Spring, Beaver Co., Utah.



Fig. 35. Cadavers of two gray fox and a bobcat abandoned after most valuable pelts had been removed. South end of Pine Valley, Beaver Co., Utah, 13 December 1969.

enlightenment through research and coordination before the objective is achieved.

An illustration of problems arising from high rabbit populations (possibly as a result of low predator numbers) is to be found in attempts at reseeding a cleared, juniper-pinyon area by the Utah State Department of Fish and Game. In 1963 they were

forced to redo some 500 acres of land initially reseeded in 1958 in the Indian Peaks region of Pine Valley. Small acreage reseeding projects in the south end of Wah Wah Valley may be doomed to failure because of the high numbers of rabbits feeding on the newly planted vegetation (Brough, 1969).

SUMMARY AND CONCLUSIONS

The Public Lands in Pine and Wah Wah Valleys have been grazed since about 1870. Evidence indicates that the lands were stocked at excessive rates for more than 30 years prior to establishment of the Taylor Grazing Act in 1934. Excessive stocking resulted in deterioration of high quality grazing plants among the desert shrubs and grasses, in the reduction of total plant cover, in the increase of less desirable native plants, in introduction of weedy and poisonous plants, and increase in extent of juniper and pinyon, and in accelerated soil erosion.

The Desert Experimental Range has provided a model for good grazing and management practices which result in improvement and maintenance of desert vegetation.

The Bureau of Land Management inherited a badly abused resource base in the 1930's, and during the period 1935 to 1950 recognized that the land was stocked at rates in excess of carrying capacity. While the trend in AUM's was downward during that period, it appears that overstocking continued largely because of economics and local custom.

During the 1950's and 1960's the lands in Pine and Wah Wah Valleys underwent adjudication and the number of AUM's was cut by 32.8 percent and 53.0 percent respectively. In that same period the Bureau

of Land Management cleared and reseeded some 14,500 acres of juniper-pinyon woodland. Thus, since the mid-1950's there has been a general improvement in the vegetation resource base.

Problem areas are still evident. These require additional study, funds, and personnel. The entire Pahvant Grazing District consists of some 5,500,000 acres. Yet, there are only six professional management personnel on the entire staff. In the Pine - Wah Wah Valleys region a single person is directly responsible for management.

Where vegetation is in poor condition due to crowding around water holes or other places, studies need to be made which will lessen the effects or do away with them.

There is need for closer cooperation and coordination of Federal, State, and County agencies to insure ease of management and lack of cross-purposes. Laws to allow more free exchange of state school lands should be enacted. The 1870 mining laws should be modified to prevent destruction of Federal lands in the name of mineral exploration. Federal and State agencies should correlate predator and fur-bearing carnivore kill with rabbit and rodent populations, and with changes in the vegetation resources which result as a consequence of carnivores killed.

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